

Part 2. GRASSHOPPER POPULATION ECOLOGY AND MANAGEMENT

4. HOW DO SPATIAL POPULATION STRUCTURES AFFECT ACRIDID MANAGEMENT?

M.G. SERGEEV^{1,2}, O.V. DENISOVA¹, and I.A. VANJKOVA¹

¹*Department of General Biology, Novosibirsk State University*

²*Pirogova St., Novosibirsk 630090 RUSSIA*

²*Institute for Systematics and Ecology of Animals*

Siberian Branch of Russian Academy of Sciences

11 Frunze St., Novosibirsk 630091 RUSSIA

Abstract

The **significance** of spatial population structures is discussed relative to locust and grasshopper management. The **general** scheme of spatial population distribution is characterized. The spatial population structures of the model species (*Calliptamus italicus*, *C. abbreviatus*, *Chorthippus parallelus*, *Ch. montanus*, *Ch. fallax*, and *Podisma pedestris*) are described for temperate Eurasia. The temporal stability of many features of local colonies is shown. The boundaries between the different parts of a population system are evaluated as being very distinct. Movements of grasshoppers (including good flyers) are limited by local landscape barriers. Approaches and procedures of acridological population studies are discussed relative to management systems for pest and rare species.

1. Problems

Management of locust and grasshopper populations is usually based on the knowledge of dynamic patterns. However, we should delineate observed differences of dynamics in different parts of a population. As we know, a population is organized in space, and the pattern of the spatial structure is usually rather complicated [1-5]. A few classic papers [6, 7] have been primarily concerned with the internal structures of local populations, their dynamics and inner organization.

Usually local populations (demes) are distributed over a species' range in concordance with natural conditions, especially the geographical landscape structure of the

Earth's surface. These populations may be connected with each other in one landscape unit or may be divided by various barriers which determine the level of gene flow. A barrier is considered to designate something which prevents the spread of animals or plants. We can describe this general pattern as the spatial population structure of a species [8]. In many theoretical studies, this population structure is termed a metapopulation [9, 10]. So the spatial population structure is a system of all local populations in the limits of a species' range (or a species' area). This approach is expected to be very valuable for understanding general ecology and biogeography of locusts and grasshoppers and for developing management strategies.

The environmental factors and the biological properties of a species are variable in time and space, so that their relations can be understood only by systematic studies of populations throughout a species' range [7]. We know of some fine examples of studies of spatial distribution of individuals, hatching sites, swarms etc. However, nothing is known of the spatial population structures for the majority of species, especially in connection with population dynamics. To solve this problem we must understand where populations are situated and how they change in space and time. When we eventually understand the exact patterns of spatial population structures, we will be able to forecast dynamic patterns in each local population, to manage each local population, and to manage migrations between populations. While this will be hard to do for tropical locusts, the approach will provide a real opportunity for managing temperate acridid species. In the future, the studies of spatial population structures will allow us to manage some local populations or parts of population systems without serious risk to the environment.

Spatial population structures can be described in a system of geographic gradients [11, 12]: (1) The latitudinal (or zonal) gradient is mainly determined by solar radiation distribution. (2) The longitudinal (or sectoral) gradient is chiefly associated with precipitation distribution, temperature amplitudes, and climatic severity which increases from coastal to central parts of continents. (3) The vertical gradient is determined by both altitudes (elevations) and gravitational flows of energy and matter. As a result, it should be related to not only mountain territories but also to each landscape system composed of connected landscapes (*e.g.*, an individual catena *sensu lato*) or other such units.

Spatial population structures can be studied and estimated at different spatial scales [1, 13]. (1) At a range level, or at a broad scale, we investigate these structures as a system of local populations throughout a species' range. We can evaluate general spatial patterns of a species' distribution relative to geographic patterns (life zone and continental sector distributions, etc.) and identify barriers that divide regional parts of a species. (2) Regional (meta)populations are parts of a species and are limited by faunistic or geographic boundaries. At a regional level, or at a medium scale, different spatial structures can be described inside each region inhabited by a species that are more or less uniform from faunistic or geographic points of view. (3) Local populations are parts of regional metapopulations and are found within the basin limits of small rivers, the landscapes of which are uniform or closely connected by energy and matter flows. As we know, at the local level, identifying paths of wandering and potential contact between populations is possible [4, 13]. The knowledge of grasshopper distribution within such small regions allows for an understanding of the pattern of populations, community organization, and

dynamics.

The main goals of this chapter are: (1) to characterize general patterns of spatial population structures of locusts and grasshoppers, (2) to show some applications of this approach by exemplifying some model species distributions, and (3) to describe the relationships of this approach to management of locust and grasshopper populations.

2. Tools

2.1. METHODS AND MATERIALS

This study is based on quantitative and qualitative data collected on regularly distributed survey areas, as well as on the analysis of earlier published works (basically for the last two decades) and specially developed range maps.

Field sampling was organized along local transects [11]. Each local transect crossed a river valley or a lake basin from a local flood plain to a watershed plain or a montane slope, in cases where local watershed plains were almost absent or fully cultivated (see Fig. 1). Local transects were distributed according to their real positions inside three geographic gradients (zonal, sectoral, and vertical). The length of local transects varied from hundreds of meters to several kilometers. Essentially it consisted of local transect sets, extended to several hundreds of kilometers. Local transects were embedded in the long (up to several hundreds or thousands of kilometers) gradient transects (*e.g.*, transzonal).

Grass landscapes and similar anthropogenic habitats along local transects were studied mainly in connection with specificity of temperate grasshoppers and locusts [2, 3, 11, 12]. Each part of local transects (low and upper flood plains, low and upper terraces, watershed plain) usually was investigated separately. Samples were also collected for different variants and units of the natural and anthropogenic landscapes. A sample area and time could vary in different landscape units and were limited by the landscape unit area.

Insects were caught by a standard net for a fixed period of time [11, 14], and the results were extrapolated to an hour. Orthopteran density was estimated from a set of plots [15, 16]; in our case usually from an area of 25 square meters. Our data show that these methods allow us to obtain stable results suitable for long-term observations and geographical studies. These methods allowed us to obtain repeatable results over a number of years and permitted precise, fine-scale definition of distributions at the population level.

The materials were collected from 1976 to 1999 in South Siberia, Kazakhstan, Kyrgyzstan, Uzbekistan, Turkmenistan, and Tajikistan. The data archived in the Department of General Biology, Novosibirsk State University, (1972-1981) were also analyzed for Siberia and Central Asia.

Three groups of relatively abundant species have been chosen to illustrate the utility of this approach. All these model groups include common species of the Palearctic. The first group consists of the Italian locust, *Calliptamus italicus* (L.), and its nearest relative *C. abbreviatus* Ikonn. of the subfamily Calliptaminae (or the tribe Calliptamini). These species are mainly connected with the semi-desert habitats of the Mediterranean and

Central Asia. The second set of species includes the group *Chorthippus parallelus* of Gomphocerinae (Gomphocerini) - *Ch. parallelus* (Zett.), *Ch. montanus* (Charp.), and *Ch. fallax* (Zub.). These species are associated with the typical meadows, meadow-steppes and dry steppes of Eurasia. The widely distributed melanopline grasshopper *Podisma pedestris* (L.) belongs to the third group. In spite of its huge range this species is distributed in many insular populations where its abundance can be high.

C. italicus is usually a good flyer and can cover relatively long distances (up to few hundreds of kilometers). Almost all other species of Calliptamus are brachypterous, although macropterous forms are sometimes abundant. *Ch. montanus* has both meso- and macropterous forms. However, migration by these species is strongly limited.

2.2. SPATIAL POPULATION STRUCTURES: GENERAL APPROACHES

The traditional approach - the analysis of spatial distributions, phylogenetic and genetic relationships between local populations inside a species range in two-dimensional geographical space [17] - is not sufficient to understand the ecology of many animals including locusts and grasshoppers. The inclusion of the vertical dimension is necessary [12, 18, 19]. The vertical axis is associated with not only general elevation but also vertical landscape structures determined by gravitational flows of energy and matter. These landscape structures can be observed as a system of slopes, terraces, depressions, etc. Such a three-dimensional approach is associated with geographic changes in habitats [12, 18] and can be expressed by vertical distributions of populations on maps of different scales.

Some earlier two-dimensional maps (especially for the breeding areas of the Desert locust (*Schistocerca gregaria* Forsk.) [20, 21] and the Moroccan locust [*Dociostaurus maroccanus* (Thnb.)] [22] are very interesting and important for understanding spatial population structures. They permit us to divide the species range into many zones with different types of population dynamics. However, in many cases, they can be interpreted as three-dimensional maps because the text description of landscape features is added. For example, Adamović [22] described the apparent restriction of the solitary form of the Moroccan locust to small spots with optimal soils and vegetation.

Previously we described three main types of species colonies on plains [3, 12]:

(1) The watershed populations are more or less diffusive, *i.e.*, they occupy all available habitats, and there are no evident barriers between local populations (Fig. 1, WP);

(2) The valley populations occur on flood plains and low (moist) terraces (Fig. 1, FL, FU, TL). As a rule, such populations may be characterized as insular or linear. The insular populations are distributed as islands with significant uninhabited areas between them. The linear pattern resembles a band associated with a linear landscape unit. Populations of this type are usually isolated from their neighbours.

(3) The slope (terrace) populations are distributed over upper and middle terraces of rivers and lakes (Fig. 1, TU).

Insular high-montane populations can be observed at high altitudes in montane regions.

As a rule, these types form a limited number of combinations in every region or locality. We described four combinations for plains [3, 11, 12]:

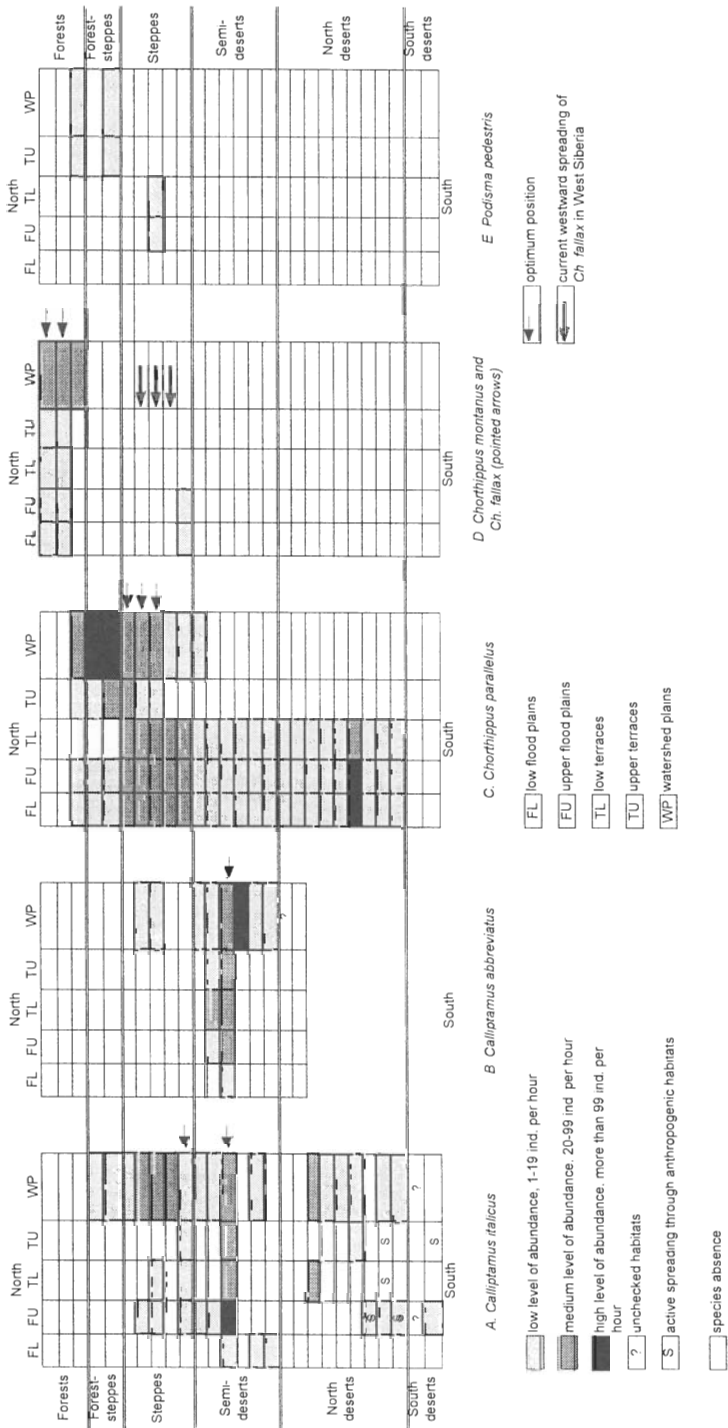


Figure 1. Population distribution of model orthopteran species along north-south transects from West Siberia to Tajikistan (A, C-E) and from the Central Siberia to Tuva (B)

1 - The **optimal or main part** is distributed over all available habitats at a high (but not extremely high) and comparatively stable level of abundance (the optimum of a range) (Fig. 1, black arrows).

2 - The **transitional part** is associated with the beginning of population dissociation (bifurcation) into the watershed and valley population subsystems. Populations are very rare or almost absent on the terraces.

3 - The **basic part** is found over watershed plains, flood plains and/or low terraces (sometimes over watersheds only); species abundance can be high locally. These areas often occupy almost all of the range.

4 - The **marginal part** is characterized by connection of populations with flood plains and low terraces; the populations are insular or linear.

The **high-montane-valley part** should be added to montane areas. There are systems of insular, linear and linear-insular local populations.

The analysis at the regional and local levels usually shows that every part of the range (especially the basic one) is a mosaic, where areas of different types of population distribution are interspersed throughout the dominating background. This is especially important for re-assessment of different ecogeographic barriers which constitute the limits for species spreading and migration. For instance, Schennum and Willey [23] have emphasized that the montane populations show a much higher degree of differentiation and discordance, and Lake Michigan acts as a natural barrier for gene flow [24]. In some cases, human activity sharply limits the spatial distribution of grasshopper populations. Conversely, new corridors for migration and colonization of previously uninhabited habitats can be established [1, 5, 25, 26 *et al.*].

2.3. TEMPORAL STABILITY OF SPATIAL STRUCTURES

Quantitative and qualitative samples of grasshoppers taken through a number of years in the comparatively uniform regions are highly correlated with each other and often have no meaningful differences [3, 4]. This seems to be consistent for temperate grasshoppers and solitary populations of locusts [7, 22]. Our studies (unpublished data) in the Central Altai Mts. have shown that population distributions and frequencies of different variants of polymorphic traits exhibit some fluctuations but stay relatively stable in most cases.

Quantitative accounts on a constant set of habitats in the vicinity of Novosibirsk were conducted to study the long-term stability of abundance levels and population distributions in 1981-1999 [27; unpublished data]. An analysis of the long-term data confirmed that the landscape distribution of *Ch. parallelus* did not change significantly [3]. In weakly disturbed habitats, its abundance varies, but maintains approximately the same level. As a whole, *Ch. parallelus* demonstrates constant preference for the steppe meadows of watershed plains. Therefore, in spite of certain variation, we contend that landscape distribution of populations and their parameters are comparatively stable for temperate grasshoppers.

2.4. SPECIES CO-EXISTENCE

Co-existence of species in every region is sustained by the differentiation of so-called "place niches" [28]; this co-existence is supposed to be a result of specific habitat elimination [29] and different species connections with succession processes [30]. The problem of competition at different levels is not solved to date, but in most cases the role of competition is not too significant [31]. Mulkern [32] analyzed multidimensional overlapping in resource utilization by prairie grasshoppers and found that there was little overlap among co-existing species.

The comparison of local population distributions of orthopteran species in the small river basins within the main biogeographical regions allows us to describe three main trends of grasshopper co-existence for temperate Eurasia [13, 33]:

(1) The majority of species inhabiting small river basins have strongly localized populations, and the density of each population is usually low. Such situations occur in the Far East and the deserts of Central Asia. There are a few species with widely distributed populations.

(2) Most species are distributed over all available habitats of the local river basin at high levels of abundance. Such forms spread through anthropogenic landscapes. As a rule, the maximum density of one species does not coincide in space and time with the maximum of others. This situation is observed in the forest-steppes and in some parts of the mountains of South Siberia.

(3) The intermediate type includes local populations distributed over a number of habitats, which are usually connected with each other. Densities can be high to very high. In the plain steppes, such species prefer local watersheds. Both in the mountains of South Siberia and in the northern part of the Central Asian mountains, these species are mainly associated with local southern slopes. On the contrary, in the southern part of these mountains, such orthopterans are linked with northern slopes.

2.5. SPATIAL POPULATION STRUCTURES OF THE MODEL SPECIES

To simplify discussion we compare spatial population structures of the model species only along a main transzonal transect which crosses the internal part of Eurasia from the West Siberian forests to the southern desert of Tajikistan and Turkmenistan (Fig. 1, A, C-E) [3, 5]. This transect crosses almost all ranges of the model species from north to south. It consists of local transect sets representing vertical landscape organization. Their positions are determined by distributions of life zones and their subzonal parts. Therefore, we can characterize the spatial population distribution along this main transect as the zonal-landscape form.

2.5.1. *Calliptamus italicus*

The Italian locust is a common species and the most important pest in the Mediterranean and Saharan-Gobian regions. Many of its outbreaks were described for these areas and for the neighbouring steppes and mountains.

The Italian locust is an intermediate form between typical gregarious and solitary

acridid species [7]. For its gregarious form distinctive migrations are described over comparatively small distances of about 100-200 km [34].

Ecological and geographical particularities of this species are described in many publications and for different parts of its range. Analysis of the main part of these studies is given by Uvarov [7], who emphasized the insufficiency of our knowledge of the Italian locust during periods between outbreaks. For the last two decades, more than 20 studies of this species were published but nearly all of these are limited to outbreak periods.

General particularities of spatial distribution. The main part of the species' range is located in the semi-desert zone where many outbreaks have been often observed and as a rule, abundance is high [5, 7]. This pattern coincides with the distribution of plants preferred by this species - xeromorphic dicotyledons like sagebrush [7, 37], as well as with the availability of the terrain used for egg laying (nearly bare, often sandy, soil) [7]. Based on available data, the Italian Locust appears to prefer landscapes with a mosaic of xeric plant cover. It is interesting to note that in spite of the overall abundance of the Italian Locust, its several restricted populations in Western Europe are critically endangered or even likely to go extinct [35, 36].

Zonal-landscape distribution over the studied transect. On the main transect, the Italian locust distinctly prefers the semi-desert of the Kazakh Uplands, or so-called Sary-Arka (Fig. 1, A). Nearly constant high abundance (observed in 1975, 1976, 1986, 1991) and distribution in all available habitats suggest that this region is optimal for the species. This area covers the semi-desert of East Kazakhstan and confirm earlier results [2, 38].

In the northern part of the transect, the Italian locust is actually distributed more widely than was indicated by Stebaev [38]. Here, it inhabits the forest-steppes on overgrazed plain pastures, but usually occurs very locally and at low levels of abundance. In the steppes, its populations occupy not only local watershed plains, but the dry parts of upper flood plains and lower terraces, and the stony southern slopes of hills. In this area, another optimal habitat of this species occurs in the dry steppes of Kulunda [2]. This habitat partly covers a zone of the dry pine forests of the Irtysh region, and outbreaks often occur here [34, 39].

The most recent *C. italicus* outbreak started in this optimal habitat in the summer of 1999. (However, in neighbouring Pavlodar Region of Kazakhstan, the outbreak began in 1997). Densities of the Italian locust increased sharply after a warm and dry May, especially in fallow fields. Its populations occupied almost all suitable habitats including openings of pine forests, fallow agricultural fields, stony slopes and wet meadows at comparatively high levels of abundance (1-5 individuals per square meter). Some agricultural fields (mainly sunflowers) were damaged. However, our data show that all studied populations are intermediate between the typical solitary and gregarious populations.

The presence of two optima near the east boundaries of Kazakhstan (main and additional) corresponds to the situation described by Stolyarov [40] for West Kazakhstan. Both optima seem to stretch east-west through the whole eastern part of the locust's range.

In the southern part of the transect, populations of the Italian locust once again

become more local. In the northern deserts, they are distributed on plain watersheds (Fig. 1, A), and their local density can be rather high. The locust's abundance decreases to the south where its main populations are associated with river valleys and lake basins. Here the Italian locust often inhabits not only sagebrush vegetation in the steppe habitats but also meadows. In this part of its range, the Italian locust is widely distributed through irrigated fields, including alfalfa, and canal borders.

Spatial population distribution of the Italian locust at periods between outbreaks both within the whole area, and on along the model transect, generally corresponds to the rule of habitat change [18]. In the northern part, the species is distributed over very dry habitats; in the central zone it prefers medium to xeric and varied habitats of the steppe and semi-desert; in the southern part, its habitats are usually localized in meso-hygrophylous areas of river valleys or in the mountains.

If the distribution of the Italian locust along the model transect is compared with the distribution of relatively well-studied grasshoppers such as the white-striped grasshopper [*Ch. albomarginatus* (Deg.)] [18] and *Ch. parallelus* [3], it becomes absolutely clear that its distribution is very different from them [3, 12]. In the first place the Italian locust dominates in the additional (steppe) optimum of the population distribution. Besides that, the Italian locust's range includes a comparatively small mountain area, where conditions for its existence are nearly optimal [5].

It is important to note that population dynamics within main and additional optima differ significantly, because they are situated in different climatic zones. In even greater degree, this is true for the marginal areas of high abundance and probably for the populations occupying different ecosystems within a small region (e.g., flood plain and watershed plain). For forecasting of the Italian locust (and other locusts) it is necessary to locate permanent survey sites in different parts of its range, including both natural and anthropogenic landscapes.

2.5.2. *Calliptamus abbreviatus*

C. abbreviatus is another species of this genus in Central and East Asia [41]. Its abundance can be rather high sometimes even reaching pest levels [42]. *C. abbreviatus* belongs to the north temperate group of the genus *Calliptamus*, more adapted to humid and cool boreal and sub-boreal conditions, but its isolation from *C. italicus* has occurred due to isolation in the Far East and Central Asia [43].

General particularities of spatial distribution. As with the Italian locust, *C. abbreviatus* prefers the dry steppes and semi-deserts with a mosaic of xeromorphic vegetation and stony soils [11, 41]. Both species are distinguished from the nearest relatives - West-Mediterranean *C. wattenwylanus* (Pantel) and Irano-Turanian *C. turanicus* Serg. Tarb. The first prefers the typical, often disturbed, Mediterranean habitats [43], and the second is mainly associated with the deserts of piedmont plains. *C. abbreviatus* is obviously adapted to conditions of the Mongolian area with maximum precipitation and corresponding growth of plants occurring in late summer. This pattern corresponds to the distribution of its preferred plants such as xeromorphic dicotyledons (sagebrush) [37].

Zonal-landscape distribution over the studied transect. Because this species is distributed in the eastern half of temperate Eurasia, it does not occur along the main transect. As a result, we used another transect for the comparative analysis of its spatial distribution. This additional transect crossed the southern part of Krasnoyarsk Region, Khakasia and Tuva Republics (Fig. 1, B).

Here *C. abbreviatus* distinctly prefers the semi-deserts of the Mongolian type (Fig. 1, B). In these semi-deserts, it is distributed through all available habitats, from flood plains to watershed plains and southern slopes. Comparatively high levels of abundance (in the second half of summer up to 300-500 individuals per hour of collecting) and distribution in all suitable habitats indicate that this region is optimal for the species.

In the northern part of the transect, in the dry steppes, *C. abbreviatus* is found in nearly all primary habitats, but its density decreases. However, in the montane steppes and forest-steppes, *C. abbreviatus* is generally absent even on the driest southern slopes. It has rare populations on the plains and arid slopes in the low part of the montane steppe belt (usually not above 1500 m), as well as in the semi-desert of the central part of Tuva. *C. abbreviatus* is not found northward.

In the southern part of the transect, its populations again become very local. In the most dry variants of the semi-desert and in the deserts, they are on the watershed plains (Fig. 1, B) and southern slopes.

In the Far East, *C. abbreviatus* is usually found in dry regions [41]. In contrast with the South-Siberian transect, its abundance here is usually low; populations are local and associated with xeric habitats, from the stony flood plains to the southern slopes. The broad amplitude of its distribution is observed in the hill area near Khanko Lake. In the northern forest-steppes of the Amur Region and in the Daurian steppes, *C. abbreviatus* occurs in xeric plain habitats and southern slopes.

In the forest regions of the Far East, in spite of wide distribution of some xeric habitats, particularly southern slopes, *C. abbreviatus* is a rare species. Only in the most southern part of the Russian Far East, is it occasionally found on dry south declivities and on the stony flood plains.

The distribution pattern of *C. abbreviatus* is similar to that of the Italian locust. However, careful analysis reveals some essential differences: (1) *C. abbreviatus* populations are distributed more locally and gravitate almost exclusively to xeric habitats with a mosaic vegetation cover and stones; (2) Unlike the other species of the genus, *C. abbreviatus* does not inhabit anthropogenic habitats. Moreover, its migratory potential is probably very limited even at the intralandscape level.

As a result, it appears that in spite of the extensive range and rather high densities in some habitats, the general pattern of its distribution is similar to many endemic species of grasshoppers with their highly localized and usually fragmented populations [1]. This makes *C. abbreviatus* a perfect species for testing the models developed in modern conservation biology relative to endemic species with highly localized populations. This type of distribution also helps to better understand the reasons for the absence of *C. abbreviatus*'s outbreaks, since typically, outbreaks are characteristic of locusts and grasshoppers with well integrated population systems. However, in the long term, changes in the ecological and climatic setting (including the anthropogenic influence) will result in

creating the conditions favourable for increasing *C. abbreviatus* abundance.

2.5.3. *Chorthippus parallelus*

The spatial population structure of *Ch. parallelus* was described by Kazakova and Sergeev [3]. The species has a classic pattern of a population distribution with an optimum in the northern steppes [12], making it suitable for spatial extrapolations.

General particularities of spatial distribution. The species is common and abundant in meadow and meadow-steppe habitats of the temperate Palaearctic. Rare cases of migrations of *Ch. parallelus* are mostly of an intrapopulation nature [44]; macropterous specimens of this species can not usually fly [45]. Our experimental data for the West Siberian forest-steppes also show that brachypterous (normal) specimens of *Ch. parallelus* do not cross forest-bush belts 10-15 m in width.

Zonal-landscape distribution over the studied transect. The northern part of the main transect is occupied mostly by scattered populations of this species associated with watershed meadows (Fig. 1, C) and flood plains. Its local abundance can be very high. Further south, in the south forest-steppe and particularly in the steppe life zone, abundance of this species is usually high in all meadow and meadow-steppe habitats. Therefore, this is an optimal area for this species.

In the southern part of the studied transect, the species is found almost exclusively in river valleys, near lakes, and in the mountains. Its populations are distributed sporadically and occupy grass meadows on flood plains and low terraces. The species' abundance is usually low but can be very high in some habitats. This means that contact between these local populations is limited.

For the plains area as a whole, a border between the steppe and the semi-desert parts of the range (*i.e.*, the border between the natural life zones associated with significant decreases of precipitation) is the most significant barrier for dividing spatial population structures. As follows from landscape distribution of populations, this transition corresponds to the change from diffusive and nearly diffusive distribution of *Ch. parallelus* to the insular distribution.

The distribution pattern of this species is suitable for spatial extrapolations. However, genetic and ecological differences between its local populations can be very significant. This means that we should study every local population of the species for exact temporal forecasting, but in practice this is impossible. Therefore, the compromise would be to study a wide set of populations in different habitats and to evaluate main types of dynamics.

2.5.4. *Chorthippus montanus*

This species inhabits the northern (boreal and subboreal) part of temperate Eurasia [11]. It prefers wet meadows with grasses.

Our data show that its optimal area lies near the northern part of the model transect (*i.e.*, in the boreal forests). The southern portion (Fig. 1, D) lies in the south of the forest zone. Some insular populations of the species are situated in the forest-steppes and the

steppes. They are very local, and species abundance is usually very low. As a result, populations of the species are sporadic and migrations between them are limited.

This pattern coincides with the species' distribution in the Russian Far East [46] where *Ch. montanus* prefers meadows of the south forests. In the mountains of South Siberia this species is mesohydrophilous [33], and has an insular population structure.

The general distribution of *Ch. montanus* differs from the distribution of similar species (Fig. 1, C-D). This is a result of ecological and evolutionary differences, probably reflecting the species' origination in the forest life zone.

2.5.5. *Chorthippus fallax*

Ch. fallax is a typical East-Palaearctic species [11]. Its range spreads westward over xeric, anthropogenic habitats, like overgrazed rangeland and road sides. It does not reach the main transect. However, in the near future, this species will probably be able to use disturbed habitats of the local watershed plains and upper terraces to spread westward in the steppe zone (Fig. 1, D, pointed arrows).

In the Kulunda steppe, *Ch. fallax* is distinctly associated with dry plots of watershed plains, terraces and flood plains. As a rule, its populations are highly localized and occur in disturbed habitats. Its abundance can fluctuate significantly.

The optimum zone of its range lies in the steppe regions of Mongolia and the South Siberian Mountains. Here the species prefers the steppe and dry meadow habitats [33]. In the dry steppes and semi-deserts, its populations are found in river valleys, from flood plains to middle terraces. However, in the Far East, its populations are distributed over mesic habitats (meadows, slopes with openings etc.) [46].

Therefore, three close species of the *Ch. parallelus* group differ significantly in their ecological preferences. *Ch. parallelus* is associated with the central part of Eurasia and prefers meadows and meadow steppes. *Ch. montanus* occupies the boreal area and prefers wet meadows. *Ch. fallax* inhabits the eastern part of temperate Eurasia and uses dry meadows and steppes. Their population distributions are usually limited by a consistent set of conditions. As a result, they occur very rarely in the same habitats at similar levels of abundance.

2.5.6. *Podisma pedestris*

This species is widely distributed in the Palaearctic. It occurs from the mountains of South Europe to East Siberia. *P. pedestris* usually prefers meadows and openings of pine forests.

This species is found in the northern part of the model transect (Fig. 1, E). Here its populations are extremely sporadic and occur in meadow openings and forest edges on watershed plains and upper terraces. In the typical steppes, *P. pedestris* is observed in meadow openings of the riverine forests. Its abundance is usually very low.

However, in some areas (e.g., in the Central Altai Mts., in some years, the abundance of this species can be extremely high [33]. As a result, local populations of *P. pedestris* can colonize new habitats and areas. Here *P. pedestris* uses anthropogenic habitats like road sides with ruderal vegetation, and cropland. In contrast, human activities in the vicinity of Novosibirsk have resulted in almost complete extirpation of local populations inhabiting the clearings of the pine forests.

2.6. PHENOTYPIC TRAITS IN SPATIAL POPULATION ANALYSIS

The analysis of species distribution allows us to distinguish parts of a species range and its population system. However, this approach is not sufficient, especially at the local level. Completely isolated populations are exceptional [7] and usually restricted to non-flying montane or island forms in specific natural conditions. Continuous populations with uniform structure are very rare too. Therefore, it may be difficult to differentiate uniform local populations solely on the basis of distribution patterns.

Investigations of frequency distribution of colour and other phenotypic traits can show more complicated relations between the different parts of population systems. The investigation of colour morph frequencies allows us to separate some parts of population systems, which can not be described by conventional methods [3].

For instance, the spatial distribution of *Ch. parallelus* in the optimal area shows that there are no obstacles for migration and gene flow. However, phenotype frequencies among valley and watershed populations demonstrate their separate status [3]. Similar local studies of good flyers, [e.g., *Bryodemus tuberculatum* (L.)], show that even a small montane river (10-15 m wide) can be a serious obstacle to migration [4].

3. Solutions

Local populations of each species can be significantly different in ecological, geographical and, probably, genetic characteristics. This is usually the case for neighbouring populations, which may require different management procedures. This means that we must evaluate these differences and these for population management.

Unfortunately, related species of locusts and grasshoppers can have different spatial population organizations. Sometimes they are similar in general distribution pattern (e.g., *C. italicus* and *C. abbreviatus*) (Fig. 1, A-B), but they are significantly different at regional and local levels.

This is important both for potential pest species and for rare grasshoppers and other orthopterans. Consequently, species with spatially discrete population systems are not suitable subjects for forecasting and modelling. Probably this is also true for typical locusts, such as the Migratory (*Locusta migratoria* L.) and the Desert locusts.

Local populations of rare species may be very different. Some of them are under the threat of extinction or critically endangered [26, 47]. Few populations can be stable for a long time at low levels of abundance [47, 48]. However, some populations of rare grasshoppers can be abundant for a long time in a very limited space. It is interesting that some local populations of pest species (e.g., *P. pedestris* or especially *C. italicus*) may be almost extinct, while others are thriving.

All this means that if we want to create a productive management system we must study dynamic patterns of the spatial population structures of each species across a range of scales from the general to the local (Fig. 2). These studies should include three main levels: general (the whole species' range), regional and local. At the general level of studies, a species range and its boundaries can be explored relative to the ecological limits

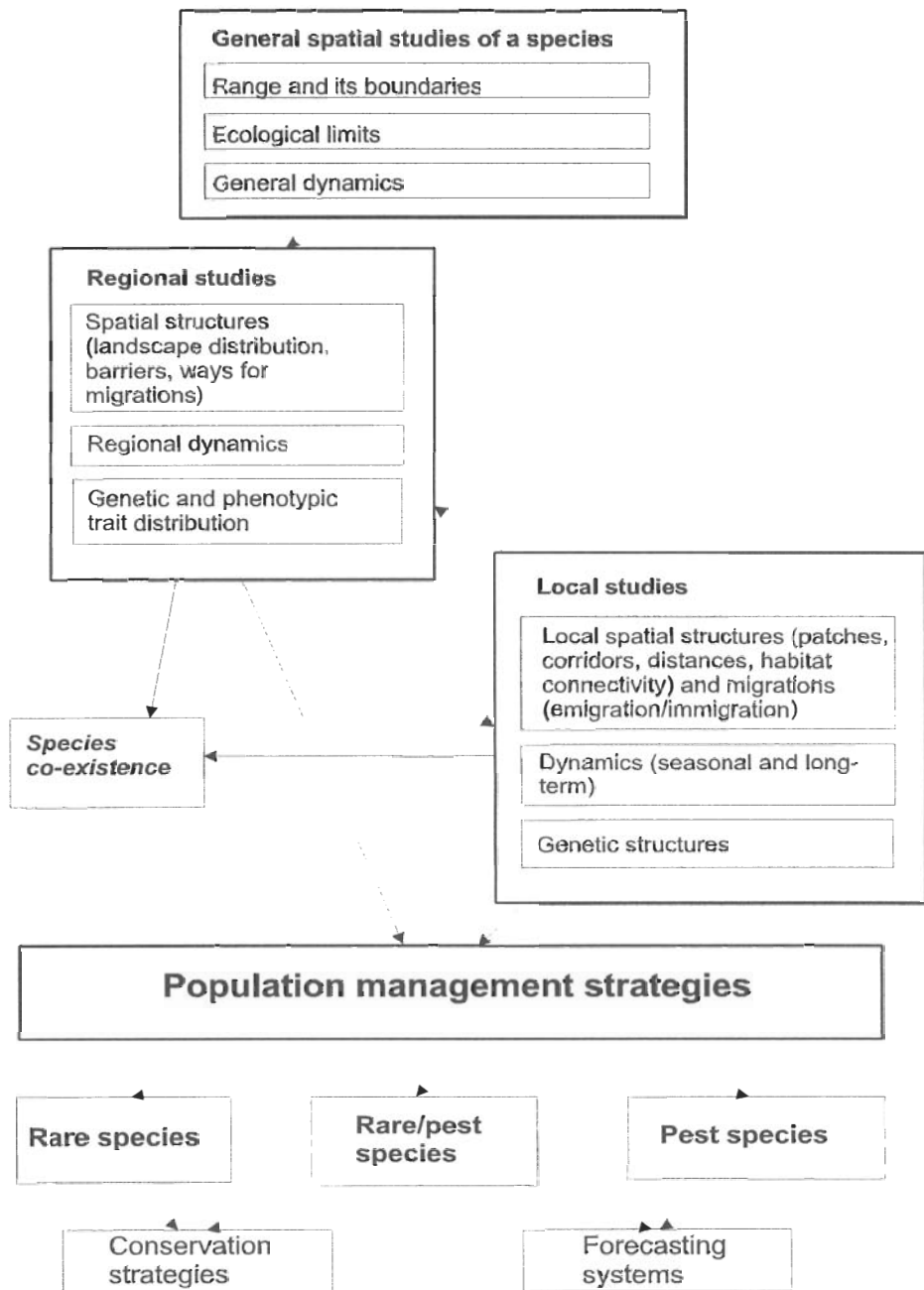


Figure 2. Procedure of spatial studies of locust and grasshopper populations for management systems

and general dynamic patterns. These data may be used to establish the main area for regional studies with approximately similar conditions (usually geographic regions and life zones).

Regional studies should include research of spatial population structures, evaluating barriers, and paths for migration, long-term dynamics, and genetic and phenotypic trait distributions. Such studies should result in the choosing of model plots for local investigations.

At the local level of study, we should assess spatial structures (patches and gaps, distances, population connections, barriers and corridors) and local migration systems (parameters of emigration and immigration) associated with a landscape matrix. We should monitor seasonal and long-term dynamics of local populations and try to evaluate their temporal patterns relative to climatic and ecosystem changes and to peculiarities of each population. At this level, some special genetic investigations should be undertaken and characters of gene flow should be estimated. Generally, a sound basis for population management strategies can be created as a result of regional and local studies.

Population management strategies are manifest as three main types (Fig. 2). The first strategy is for rare forms. As a result, conservation strategies can vary in different parts of a range. The second one is for typical pest species. The results of spatial and temporal research at different scales are important for forecasting, and spatial patterns are very important in optimizing the use of insecticides, especially fogger treatments. In this case, the optimal results of insecticide applications are only possible if control programs are strongly associated with spatial heterogeneity of populations [49, 50]. The third strategy is for forms with populations distinguished by their status in different areas. In some territories, such species are subjects for conservation measures and in others their dynamics and distribution must be managed to prevent damage.

4. Acknowledgements

We wish to express our sincere thanks to Professor A. Joern and Dr. I. Sokolov for valuable comments. We thank the Russian State Programme "Universities of Russia" (grant 1759), the Russian State Programme "Biological Diversity", the Russian Foundation for Basic Research (grant 97-49399), and the Federal Programme "Integration" (projects 274 and 275) for vital financial support.

5. References

1. Sergeev, M.G. (1997) Ecogeographical distribution of Orthoptera, in S.K. Gangwere, M.C. Muralirangan and M. Muralirangan (eds.), *The Bionomic of Grasshoppers, Katydid and their Kin*, CAB International, Oxon and New York, pp. 129-146.
2. Sergeev, M.G. (1997) Metapopulations of locusts and grasshoppers: spatial structures, their dynamics and early warning systems, in S. Krall, R. Peveling and D. Ba Diallo (eds.), *New Strategies in Locust Control*, Birkhauser Verlag, Bazel et al., pp. 75-80.

3. Kazakova, I.G. and Sergeev, M.G. (1992) Spatial organization of species populations in system of short-horned grasshopper *Chorthippus parallelus*, *Zhurnal Obstshej Biologii* **53**, 373-383. (In Russian with English summary)
4. Kazakova, I.G. and Sergeev, M.G. (1997) About determination problem of grasshopper population boundaries, *Sibirskii Ecologicheskii Zhurnal* **4**, 315-321. (In Russian)
5. Sergeev, M.G. and Vanjkova, I.A. (1996) Zonal-landscape distribution of populations of the Italian Locust *Calliptamus italicus* L. (Insecta, Orthoptera, Acrididae), *Sibirskii Ecologicheskii Zhurnal* **3**, 219-225. (In Russian)
6. Richards, O.W. and Walford, N. (1954) Studies on the ecology and population dynamics of British grasshoppers, *Anti-Locust Bulletin* **17**, 1-182.
7. Uvarov, B.P. (1977) *Grasshoppers and Locusts. A handbook of general acridology*. Vol. 2, Centre for Overseas Pest Research, London.
8. Shilov, I.A. (1977) *Ecological and physiological base of population relations of animals*, Moscow University Press, Moscow. (In Russian)
9. Levins, R. (1970) Extinction, in M. Gustenhaver (ed.), *Some Mathematical Questions in Biology*, Vol. 2, Providence, Rhode Island, pp. 77-107.
10. Hanski, I. (1998) Metapopulation dynamics, *Nature* **396**, 41-49.
11. Sergeev, M.G. (1986) *Patterns of Orthoptera distribution in North Asia*, Nauka Publ., Novosibirsk. (In Russian)
12. Stebaev, I.V., Sergeev, M.G. (1982) The internal landscape-population structure of area, as exemplified by Acrididae, *Zhurnal Obstshej Biologii* **43**, 399-410. (In Russian with English summary)
13. Sergeev, M.G. Biological diversity of Orthoptera in the North-East Palaearctic: Population distribution, *Sibirskii Ecologicheskii Zhurnal* **1**, 547-554. (In Russian)
14. Gause, G.F. (1930) Studies on the ecology of the Orthoptera, *Ecology* **11**, 307-325.
15. Riegert, P.M. (1968) A history of grasshopper abundance surveys and forecast of outbreaks in Saskatchewan, *Memoir of Entomological Society of Canada* **52**, 3-99.
16. Onsager, J.A. (1977) Comparison of five methods for estimating density of rangeland grasshoppers, *J. of Economic Entomology* **70**, 187-190.
17. Tupikova, N.V. (1969) *Zoological mapping*, Moscow University Press, Moscow. (In Russian)
18. Bey-Bienko, G.J. (1930) The zonal and ecological distribution of Acrididae in West Siberian and Zaisan Plains, *Bulleten Zaststshity Rastenii. Entomologia* **1**(1), 51-90. (In Russian with English summary)
19. Zenkewitch, L. and Brotzky, V. (1939) Ecological depth-temperature areas of benthos mass-forms of the Barents-sea, *Ecology* **20**, 569-576.
20. Davies, D.E. (1952) Seasonal breeding and migrations of the Desert Locust (*Schistocerca gregaria* Forskål) in North-Eastern Africa and the Middle East, *Anti-Locust Memoir* **4**, 1-57.
21. Fourtescue-Foulkes, J. (1953) Seasonal breeding and migrations of the Desert Locust (*Schistocerca gregaria* Forskål) in South-Western Asia, *Anti-Locust Memoir* **5**, 1-36.
22. Adamović, Z.R. (1959) The Moroccan Locust (*Docioctavrus maroccanus* Thunberg) in North Banat, Serbia, *Bull. Mus. Hist. Nat. Belgrade, Serie B* **13**, 1-123.
23. Schennum, W.E., Willey, R.B. (1979) A geographical analysis of quantitative morphological variation in the grasshopper *Arphia conspersa*, *Evolution* **33**, 64-84.
24. Willey, R.B. (1987) Pattern of gene flow disruption in the evolution of the genus *Arphia* (Acrididae: Oedipodinae), in B. Baccetti (ed.), *Evolutionary Biology of Orthopteroïd Insects*, Ellis Horwood Ltd, Chichester, pp. 592-600.
25. Samways, M.J. and Sergeev, M.G. (1997) Orthoptera and landscape change, in S.K. Gangwere, M.C. Muralirangan and M. Muralirangan (eds.), *The Bionomic of Grasshoppers, Katydid and their Kin*, CAB International, Oxon and New York, pp. 147-162.
26. Sergeev, M.G. (1998) Conservation of orthopteran biological diversity relative to landscape change in temperate Eurasia, *J. Insect Conservation* **2**, 247-252.
27. Stebaeva, S.K. and Sergeev, M.G. (1995) Structure of collembolan and chortobiont communities in grass urboecosystems, *Polskie Pismo Entomologiczne* **64**, 199-206.
28. Clarke, G.L. (1954) *Elements of ecology*, Wiley & Sons, New York and Chapman & Hall, London.
29. Elton, C.S. (1930) *Animal ecology and evolution*, Clarendon Press, Oxford.
30. Buckley, R. (1983) A possible mechanism for maintaining diversity in species-rich communities: an addendum to Connell's hypotheses, *Oikos* **40**, 312.

31. Evans, E.W. (1992) Absence of interspecific competition among tallgrass prairie grasshoppers during a drought, *Ecology* **73**, 1038-1044.
32. Mulkern, G.B. (1982) Multidimensional analysis of overlap in resource utilization by grasshoppers, *Transactions of the American Entomological Society* **108**, 1-9.
33. Kazakova, I.G. and Sergeev, M.G. (1992) Regularities of distribution of the Orthopteroids populations in natural and anthropogenic landscapes of mountain depressions in Southern Siberia, *Entomologicheskoe Obozrenije* **71**, 731-741. (In Russian with English summary) (English translation - *Entomological Review* **72**, 70-80)
34. Bunin, L.D. (1979). The Italian Locust (*Calliptamus italicus* L.) in the soil-saving agriculture zone in East Kazakhstan and development of treatments, Ph.D. Thesis, Leningrad. (In Russian)
35. Wallaschek, M. (1992) Stand der faunistischen Erfassung der Geradflügler (Orthoptera s.l.) in Sachsen-Anhalt *Articulata* **7**, 5-18.
36. Jürgens, K. and Rehding, G. (1992) Xerothermophile Heuschrecken (Saltatoria) im Hegau - Bestandssituation von *Oedipoda germanica* und *Calliptamus italicus*, *Articulata* **7**, 19-38.
37. Pshenitsyna, L.B. (1987). Food preference of grasshoppers relative their pressing on the steppe ecosystems, Ph.D. Thesis, Novosibirsk. (In Russian)
38. Stebaev, I.V. and Kozlovskaya, E.B. (1979) Patterns of quantitative distribution of complexes of steppic and meadow pest grasshoppers in the Irtysh region and South-East Kazakhstan relative to regionalization of their potential pest activity, in I.V. Stebaev (ed.), *Voprosy ekologii*, Novosibirsk State University, Novosibirsk, pp. 31-51. (In Russian)
39. Bugaev, G.S. (1977) Habitat distribution of grasshoppers in the zone of band pine forests in North-East Kazakhstan, *Vestnik sel'skokhoziastvennoi nauki Kazakhstana*, N6, 37-40. (In Russian)
40. Stolyarov, M.V. (1974) The Italian Locust (*Calliptamus italicus* L.) in West Kazakhstan, *Trudy Vsesojuznogo entomologicheskogo obshchestva* **57**, 98-111. (In Russian)
41. Sergeev, M.G. and Vanjkova, I.A. (1999) Zonal-landscape distribution of *Calliptamus abbreviatus* (Orthoptera, Acrididae), *Zoologicheskii Zhurnal* **78**, 31-36. (In Russian with English summary)
42. Mistshenko, L.L. (1972) Order Orthoptera (Saltatoria), O.L. Kryzhanovskii and E.M. Dantsig (eds.) *Nasekomye i klestshi - vrediteli sel'skhozjastvennykh kultur* **1**, Nauka Publ., Petersburg, pp. 16-115. (In Russian)
43. Jago, N.D. (1963) A revision of the genus *Calliptamus* Serville (Orthoptera: Acrididae), *Bull. Brit. Mus. (Natur. Hist.) Entomology* **13**, 289-350.
44. Köhler, G. and Brodhun, H. (1987) Investigation on population dynamics in Central European grasshoppers (Orthoptera: Acrididae), *Zool. Jb. Syst.* N114, 157-191.
45. Ritchie, M.G., Butlin, R.K., and Hewitt, G.M. (1987) Causation, fitness effects and morphology of macropterism in *Chorthippus parallelus* (Orthoptera: Acrididae), *Ecological Entomology* **2**, 209-218.
46. Stebaev, I.V., Murav'eva, V.M., and Sergeev, M.G. (1988) Specificity of ecological standards of the Orthoptera in landscapes with herbaceous vegetation in the Far East, *Entomologicheskoe Obozrenie* **67**, 241-250. (In Russian with English summary) (English translation - *Entomological Review* **68**, 1-10)
47. Ingrisch, S. and Köhler, G. (1998) *Die Heuschrecken Mitteleuropas*, Westarp Wissenschaften, Magdeburg.
48. Chernyakhovskiy, M.E. (in press) Can micropopulation management protect rare grasshoppers?, in J.A. Lockwood, A.V. Latchinsky, M.G. Sergeev (eds.) *Grasshoppers and Grassland Health*, Kluwer Academic Publishers, Dordrecht (this volume)
49. Sobolev, N.N. and Sergeev, M.G. (1985) Population dynamics of grasshoppers in the agrocoenoses of North Kazakhstan, G.S. Zolotareno (ed.), *Antropogennyye vozdeystviya na soobshchestva nasekomyh*, Nauka Publ., Novosibirsk, pp. 96-104. (In Russian)
50. Sergeev, M.G., Bugrov, A.G., Kazakova, I.G. and Sobolev, N.N. (1988) Regulation of population dynamics of grasshoppers in agrocoenoses with aid of the aerosol fogger, in G.S. Zolotareno (ed.) *Landshaftnaya ekologiya nasekomyh*, Nauka Publ., Novosibirsk, pp. 63-69. (In Russian)