

Metapopulations of locusts and grasshoppers: spatial structures, their dynamics and early warning systems

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Summary. A metapopulation analysis allows us to distinguish acridid groups with similar relations to ecological factors, including landscape heterogeneity, to determine the possible paths and barriers for dispersion and to describe landscape differences in dynamic patterns. The boundaries between the different parts of a metapopulation seem to be very distinct. Often movements of grasshoppers (including good flyers) are limited by the frontiers of the local landscape.

Résumé. L'analyse des metapopulations permet à distinguer les groupes des acridiens avec ressemblant relations à facteurs écologiques, dont notamment hétérogénéité des paysages, déterminer les voies possible et barrières de diffusion et décrire les différences de paysage en régularités dynamiques. Il se suppose que les frontières entre différents parts des metapopulations sont très distincts. Souvent déplacements des acridiens, dont notamment bien volants, limitent par les frontières des paysages local.

Introduction

Many problems of modern biogeography and ecology may be solved by studying population distributions over species ranges. A number of classic papers (Richards and Waloff 1954; Uvarov 1977) considered not only the internal structures of some local populations but also their dynamics and inner organisation. As a rule, local populations (dems) are distributed over a range in accordance with natural conditions, especially landscape structures. Exchange usually occurs via migrant individuals, but a level of gene flow is often determined by different barriers (mountains, rivers, boundaries between terraces etc.). This kind of population distribution is called a *metapopulation* (Levins 1970) or a *spatial population structure* (Shilov 1977) and thus describes a system of local populations of a species within the limits of its range (area). This approach is expected to be very useful both for general ecology and biogeography of locusts and grasshoppers and for developing early warning systems. Uvarov (1977: 445) emphasized "both the environmental factors and the biological properties of a species are variable in time and space, so that their mutual relations can be understood only by systematic studies of populations of a species in all its stages throughout its total distribution area, usually comprising a

range of habitats, and extending over a period of years. Such an approach is difficult in practice, but this should not be a reason for abandoning it as an ideal goal." To date, the principal spatial organisation, especially the dynamics, of species metapopulations remains unknown, because to solve this problem we have to establish where population structures, including inter- and intrapopulation boundaries of different ranks and migration paths, are located and how and why they change in space and time.

Material and methods

The samples were collected from 1976 to 1992 in southern Siberia, Kazakhstan, Kirgizstan, Uzbekistan, Turkmenistan, Tajikistan and the North Caucasus. Two methods were mainly adapted for abundance estimation: capturing individual insects for a fixed time with a net (Gause 1930; Kashkarov 1933; Sergeev 1986), and estimating densities in small sample plots during a survey (Kashkarov 1933; Riegert 1968). A sample area and time could vary in different landscape units and were limited by landscape unit area. Usually insects were caught for 10–40 min with a standard net within 200–500 m² and densities were estimated over an area of 25 m². About 200,000 specimens belonging to 338 species of Orthoptera were analysed. These were collected during 3000 quantitative surveys using nets. We exclude data for outbreaks.

Calliptamus italicus (L.) (the Italian Locust) and *Chorthippus parallelus* (Zett.) have been chosen as the main model species. Both are the common and abundant species of the Palaearctic. The former is mainly connected with the semi-desert biotopes of the Mediterranean and Central Asia; the latter is distributed over the meadows and meadow steppes of Europe, and North and Central Asia.

Spatial structures and metapopulations of model species

We have previously described the four principal parts of a distribution area (range) of a species (Stebaev and Sergeev 1982; Sergeev 1986; Stebaev et al. 1989; Kazakova and Sergeev 1992): (1) the *main part*, within the limits of which a species is distributed in abundance over all available habitats (the optimum of a range) (Fig. 1, H); (2) the *transitional part* (K) associated with the beginning of population dismemberment (bifurcation) into the watershed and valley colonies; (3) the *basic part* (C), where the species populations are found over watershed plains and flood plains or/and low terraces, sometimes over watersheds only, species abundance may be

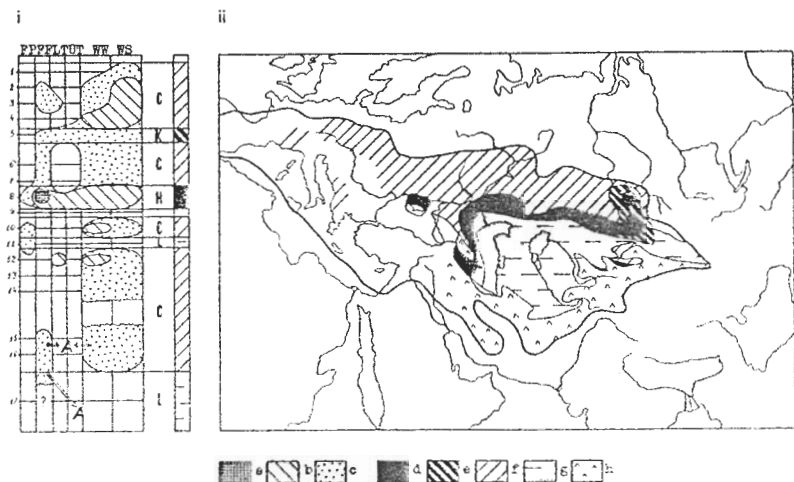


Figure 1. Colony distribution of *C. italicus* (i, landscape scheme for the eastern part of the range along the profile from Omsk to South Tajikistan; ii, map of general metapopulation structure).

a–c levels of abundance (a, more than 0.5; b, 0.1–0.5; c, less than 0.1 per square metre);

d–h parts of range (d, main; e, transitional; f, basic; g, marginal; h, montane)

A spreading through anthropogenic ecosystems;

H, K, C, L parts of range (see text);

FP low flood-plains; FF, upper flood-plains; LT, low and UT, upper terraces; WW and WS, watershed plains (WW, upland; WS, non-drained plains);

1–17 investigated transects (1, northern steppe; 2–4, typical steppes; 5, southern steppe; 6–8, semi-deserts; 9–14, northern deserts; 15–17, southern deserts).

high locally; (4) the *marginal part* (L) characterized by connection of colonies with flood plains and low terraces, and insular or linear populations. Although not always the case, both model species (*C. italicus* and *C. parallelus*) have a well-described population structure with a full set of distribution area parts (cf. Stebaev and Sergeev 1982; Stebaev et al. 1989; Kazakova and Sergeev 1992).

C. italicus is a common species in the Mediterranean and the semi-deserts and the deserts of Central and East Asia (Fig. 1). Many outbreaks have occurred in these areas and in the neighbouring steppes and mountains. Comparison of a set of transects including a number of sample plots from the local watershed plain to the flood plain allows us to describe the distribution pattern of *C. italicus* colonies along the profile from Omsk in South Siberia to Dusti in South Tajikistan (Fig. 1.i).

The main part (H) of the species range is in the limits of the semi-desert zone (Fig. 1.i, 8). There is its optimum where many outbreaks have been observed intermittently. As a rule, species

abundance is great. The transitional part (K) is situated in the southern steppe (Fig. 1.i, 5) and the basic ones – in the northern and typical steppes (1–4), the semi-deserts (partly) (6, 7) and the deserts (partly) (10, 12–16). Here the populations of *C. italicus* are associated with water-sheds, the slopes of low mountains, and sometimes with dry parts of low terraces (e.g. natural levees or scroll dunes). Species abundance may be high locally. Sometimes the outbreaks may be observed. The marginal part (L) of the range is observed in some deserts of Central Asia where the species colonies are distributed over flood plains (including meadows) and low terraces (Fig. 1.i, 11, 17). In agricultural landscapes, *C. italicus* usually spreads through irrigated fields (especially alfalfa) (Fig. 1.i, A). Outbreaks may develop.

Comparison of this profile with additional profiles and some published data (see Sergeev 1986) permits us to create a map of the general metapopulation structure of *C. italicus* (Fig. 1.ii). The local optima of *C. italicus* are in the sandy steppes of western Siberia and the Irtysh River basin and in the piedmont plains of the Tien Shan Mountains. The basic parts of its metapopulation are chiefly confined to the steppes, to the European forest-steppes and forests (partly), and also to the Mediterranean region. In the Turanian Plain, *C. italicus* mainly inhabits river valleys. In mountain regions, *C. italicus* often inhabits the local southern slopes. These population groups are isolated from the populations of the plain. An especially significant difference is observed in the southern part of Central Asia where two subspecies of *C. italicus* co-exist: short-winged *C. i. reductus* (in the mountains) and normal *C. i. italicus*.

The metapopulation structure of *C. parallelus* was described by Kazakova and Sergeev (1992). This species has a comparatively correct pattern of colony distribution with an optimum in the northern steppes, and thus is suitable for spatial extrapolations. On the other hand, *C. italicus* has some additional local optima (Fig. 1), and its metapopulation should be studied more closely.

Spatial features of dynamics

Dynamic patterns are variable in the different parts of species ranges. This is true both for locusts and for grasshoppers. For example, in the northern Siberian steppes, maximum grasshopper abundance usually occurs in the middle of summer. But in the southern steppes, semi-deserts and deserts, it may be at the beginning of summer. Both in central Yakutia and in the steppe, forest-steppe and semi-desert regions, outbreaks of non-swarming grasshoppers and *C. italicus* (in the steppes and the semi-deserts) begin after droughts. In the deserts, the outbreaks are chiefly connected with above-average annual precipitation, especially with spring

rains. Our unpublished data allow us to propose that the beginning of each outbreak is usually confined to a definite type of microhabitat. For example, *C. italicus* is clearly associated with sagebrush plots in the steppes and semi-deserts and with highly localised meadow flood plains in the deserts.

Our data also allow us to propose that the dynamics of *C. italicus* and grasshoppers may be very different in neighbouring habitats (Sergeev et al. 1988; Sergeev, unpublished data; see also Kopaneva and Dorokhova 1987). It is unlikely to result from species migrations, because the majority of species do not significantly change their local habitat distribution during seasons and years (Sobolev and Sergeev 1985). In central Kazakhstan, in non-outbreak years, the local movements of *C. italicus* are mainly connected with male wanderings. Often, observing individuals in unusual habitats is simply the result of their moving from one favourable site to another (Sobolev and Sergeev 1985).

Conclusions

Distribution of biotopes available for grasshoppers and locusts allows them to inhabit regions and landscape units (including anthropogenic) more or less widely but mainly not at random. On the other hand, important eco-geographical barriers are essential not only for limiting the spreading of whole species but also for metapopulation differentiation. In addition, observed patterns may change essentially at various scales of study. The general results of insecticide application by an aerosol fogger are evidently and strongly associated with spatial heterogeneity of species colonies (Sobolev and Sergeev 1985; Sergeev et al. 1988). So creating a system of early warning thus requires studying the spatial and temporal variations of the landscape and the geographical units inhabited by the metapopulation of each species. Investigations should be long-term and should also examine the organisation of acridid communities. The current emphasis on outbreaks needs to be supplemented with study of conditions between outbreaks, especially in connection with the organisation of populations and communities in space and time.

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