Types of spatial distribution and the mechanism of population dynamics of terrestrial vertebrates

By N.P. Naumov

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By the term "population dynamics" of animals we usually understand the population changes in time and the causes of it we see in the direct or indirect effect upon the multiplication and mortality of the individuals of the meteorological factors, food supply, activity of enemies, parasites and competitors. Recently the interest in intrapopulational relations and ratios is growing continuously (Chitty, 1955, 1957; Naumov and Nikolsky, 1962; Davis and Golley, 1963; Calhoun and Christian, 1963).

Enormous quantity of reliable information is accumulated supporting the importance of the above-enumerated factors. Among the latter, for terrestrial animals living in a highly changeable medium the importance of the external physical conditions is stressed, particularly of the climate and weather (Chapman, 1928; Uvarov, 1931; Bodenheimer, 1958). However, the important part played by the biocenotic
and population conditions is proved convincingly for these animals (Elton, 1927; Formozov, 1935). Results of four ecological conferences that took place in Kiev in 1940, 1950, 1954 and 1962, give a certain idea concerning this problem in our country.

Today, we not merely have a relatively correct idea of the general causes and mechanisms of the changes in the animal population in time, but in many cases are capable of predicting them. The physiological, biochemical and ecological mechanisms changing the conditions and behaviour of animals and the structure of their population, become known more and more accurately and profoundly.

When determining the tendencies of these changes, however, as a rule, one does not succeed in predetermining their quantitative expression. But it is exactly the quantitative expression which is necessary for the prognosis of the appearance of the pests, numbers of disease carriers, or of commercial animals. A mere predetermination of the "tendencies" is not enough; it is proper to remind that "predictions" even given at random and without any theory or understanding of the phenomena gives 50% of "agreement". Having many proved facts - "components" of the population theory, we still do not have the theory itself, which cannot be created without the aid of contemporary mathematics.

Everybody agrees that the dynamics of the numbers also expresses and quantitatively reflexes the interrelation between
the population and the medium. The foundation of this interrelation can be nothing but a biological cycle of materials mainly carried out by means of various aspects of food relations (both direct, and converse). It is exactly these relations that connect the species (their populations) into communities and ecosystems corresponding to local conditions. In the communities, in the biocoenoses all the intraspecial and interspecial connections, as well as the relations to the nonliving nature, were formed as mechanisms directly ensuring or regulating the material cycle. Of particular interest from this point of view are the mechanisms stabilizing the numbers of animals.

Studies of the multiplication and mortality have shown that their changes are mainly of adaptive and regulatory character (S. Sevetsov, 1941; Nikolsky, 1953; Naumov and Nikolsky, 1962). But as D. Lack (1954) pointed out justly, these changes alone ensure neither a sufficient stability of a population, nor any continuity of its existence. Therefore the mobility of the animals, their migrations and relations between their groupings occurring during the same are attracting still more and more attention. It became more and more evident that the population dynamics is a phenomenon developing not merely in time, but also in space (territory), and having special territorial mechanisms to which still not enough attention was given.

However, the importance of their role is beyond doubt.
In 1936, we noticed the importance of the so-called survival stations, or habitats of the maximum stable micro-populations of animals (Naumov, 1936). The territorial peculiarities of the population dynamics of rodents turned out to be a complex phenomenon (Naumov, 1945) that, in particular, has considerable importance for the understanding of natural focality of the diseases (Naumov, 1954, 1964).

The most extensive and complete data available to the author concern the population dynamics of the desert rodent - the large gerbil (Rhombomys opimus Licht.) a widely occurring background species in the deserts of the Central Asia and Kazakhstan, where this rodent is considered to be the main carrier of the plague.

The gerbils live exclusively on light soils (sand, sandy loam and light loams); they construct composite burrows that cover from several tens to hundreds, and even thousands of square meters. In sandy loams this structures are deep (up to 2 meters and more), many-storied, extremely solid, with a stable microclimate ensuring good hibernation. In harder soils the gerbils build shallow and therefore relatively weak burrows, where it is cold during frost and hot during summer. In more or less loose sand (in dunes the large gerbils do not live at all) their burrows are also unstable (Dubyansky, 1963). In the burrows
of the large gerbils live numerous cohabitating-tenants, both vertebrates and invertebrates, including numerous parasites - carriers of the plague microbe (fleas). A single animal or a gerbil family is usually utilizing several colonies gradually moving from one to another. Individual or family sections may overlap, thus, a burrow vacated by one family may be soon occupied by neighbours. The animals mark the burrows used presently by them by building a small earthen hillock in front of the entrance on top of laid excrementa. Usually they rub their bellies against this hillock. They have aromatic glands upon their bellies. Thus, a visual mark also becomes an olfactory one.

In the spring the burrow is, as a rule, occupied by a pair of animals (male and female) or by a single animal. The males act more independently and often visit the sections of neighbouring females. After appearance of a litter, when the juveniles grow bigger, the female leaves them and moves to a nearby unoccupied burrow. The males move at the same time. When grown the litter disintegrates and the young ones disperse usually to considerable distances (up to 12-17 kilometers during several months), sometimes even outside the boundaries of the parental settlement (population). Thus, the re-grouping of the population takes place periodically.

As a rule, in different biotopes, the dimensions of the individual family section are not identical, as well as
the rate of burrow changing within the confines of the section, the general mobility of the animals and the character of their distribution in the territory. All these factors determine the territorial structure of the population, i.e. the type of the gerbil settlements. In the Ural region five basic types of the settlements of the large gerbils may be segregated. They differ in the peculiarities of the population dynamics caused by the territorial structure of the population and by the character of the interrelations of the intrapopulational groupings.

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**Fig. 1.** Scarce settlements of large gerbils upon a plateau covered by *Salsola arbuscula*.

Circles indicate burrows of gerbils.

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1. *Scarce uniform (diffusive) settlements* originate on a water-shed to the north of an ancient valley of the rivers Syr-Darya and the lower course of the Sarysu (fig. 1). The
biotopes of this type are homogeneous and occupied by uniform *Salsola arbuschula* and sage-saltwort associations. Food resources are not abundant and the soil is not favourable to set up complex and stable burrows. The latter are very small here and distinguish themselves in having a little lived-in, "young" outside appearance with almost unchanged primary vegetation. These are temporary settlements with a low and very unstable population of animals, they are only inhabited during years when the population numbers rise in the basic populations.

2. To a certain degree the settlements in the focal sands in the Western Kyzylkums are of similar type (fig. 2). The composite fine mosaic of the vegetation groupings ensures a variegated and sufficiently abundant fodder to the animals, although the loose soil of the predominantly eolian sands is not very favourable for building composite and solid burrows. The mosaic of the landshape elements being uniform along

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**Fig. 2.** Settlement of the gerbils in the row-focal sands of the Western Kyzylkums (according to Sharap-kova, Dyatlov, Timkina and Serzhanov, 1958).

1 - sand hills and rows, 2 - depressions, 3 - burrows of gerbils.
the entire length of the biotope, does not contribute to a subdivision of the settlement into individual elementary populations. The density of burrows here is rather high, approximately one per one hectar, but the numbers of the animals, although high at times (more than 10 animals per one hectar) is not stable (Sharapkova, Dyatlov and others, 1958). After rises the population (the number of animals) usually drops sharply and during several (2-3) years may remain under conditions of deep depression (fig. 3), because of unfavourable fodder conditions (particularly because of the drought) and an extensive occurrence of infections contributed by no division in population settlement and high intrapopulational contact of the animals (Naumov, 1954; Kulik, 1955). An indication of the instability in the population numbers may serve the poorly lived-in appearance of the burrows, among which "new" ones predominate. A recuperation of the numbers after a depression in this settlement takes place to a considerable degree through settlement from the side, particularly along the boundaries.

3. The band-like settlements in their most typical form are restricted to the northwestern Ural area with its table and residual outcrop relief formed by numerous dry valleys and gulleys (fig. 4). The gerbils settle here along the slopes of table residual outcrops and particularly along the valleys and gulleys (fig. 4). A very sectionized relief forms a complex mosaic of the vegetation cover. But
Fig. 3. Fluctuations in the gerbil population numbers (percentage of the populated burrows) in band-like (A) and in solid (B) settlements (according to Naumov and others, 1960).

Fig. 4. Band and rosary-like settlement of large gerbils in a dry valley (northwestern Ural region). A portion of a settlement.

1 - sagebrush and motley grass associations, 2 - biyurgunniks; 3 - burrows of gerbils.

Individual elements of the landscape are represented here by relatively large massifs only a part of which groups around the erosion furrows and is suitable for gerbil habitat.

*) biyurgunniks - areas covered with Anabïs salsa /a semishrub/.
In such areas the animals are able not merely of finding abundant and variagated fodder during the warm period of the year, but also to build deep and solid burrows. Therefore, the numbers of the animals in these areas are high reaching 3-5 burrows and 25-40 animals per one hectare (at the peak of the population). However, the average density of the settlement is low, because the major part of the territory is unsuitable for the life of the gerbils.

Even within the confines of valleys and gulleys, the "bands" of settlement are actually interrupted into individual "rosaries" by usuitable sections that sectionize the valley settlement into a number of relatively independent elementary populations. The size of the territory occupied by each of them are sufficient for habitation of tens, sometimes hundreds of families. Naturally, these are not large groupings. They are not isolated from each other. The numbers of the animals in the band-rosary settlements are stable owing to the variety of food, good burrow-shelters and unfavourable conditions for the distribution of infections (see fig. 3) because of the division of the population into elementary groupings. To these settlements are attached rather stable elementary foci of plague (Naumov, 1964). Their establishment here is also facilitated by abundance and rich composition of cohabitants - tenants.

4. The Karakums near the urals located at the location of the former Turgay strait are occupied by one
of the most numerous and stable settlements of large gerbils. This settlement has simultaneously both an insular, and an uninterrupted character. The uninterruptedness is expressed in the fact that almost the entire territory is populated by this animals. However, section very densely populated with gerbils are distinctly segregated - the "foci" surrounded by scarce settlements (fig. 5). The "foci" (or "nuclei") have a composite structure. Their territory consists of a mosaic of sandy loam bed ridges of alluvial origin occupied by takyrs (desert soils) along the remains of old river beds, near-takyr loam flatlands and sections of hillocky eolian sands. Each of these sections occupies considerable areas covering hundreds and thousands of hectares; monotype sections of the mosaic landscape are considerable and each of such sections is populated by its elementary population of the gerbils. (fig. 6). Usually thousands of families occur in it. The high numbers of animals in a "focus" of population are explained by a combination of landscape elements ecologically favourable to them. In the "focus" of the settlement. The base of the complex is composed by bed ridges of alluvial sandy loams rich on fodder plants and permitting construction of particularly solid and complex burrows. It is here that the main portion of the animals hibernates. It is also here that in the spring females bring their first litters and after that the major part of adult animals migrates to neighbouring sections.
When the first litters disintegrate a portion of the young ones also migrates there. At the same time, in areas surrounding the place of hibernation the multiplication continues and owing to this the numbers of the gerbils increase sharply. However, in fall and at the beginning of the winter, many
animals migrate from here to the wintering places. Only few individuals survive till spring of those that stay in the temporary burrows for the winter. This seasonal population exchange between the wintering places and the surrounding sections ensures the high and stable numbers at the centre of the settlement, while along the peripheries of the settlement the numbers are subject to considerable fluctuations (fig. 7). Sufficiently large dimensions of the elementary populations and their variety ensure the constant interaction, high level and general stability of the population numbers of these animals in these settlements.

5. Settlements in the alluvial flatland of Daryalyktyr, which also represent a mosaic of various biotopes, are distinguished by their low extension, as well as, by their low and unstable numbers. An explanation to the above may be found in a different character of the mosaic of the landscape distinguished by a high percentage of totally uninhabitable area (takyrs and biyurgûnniks) and by a small-insular character of landscape elements suitable to the gerbils (sandy and sandy loam islands and beds). On each of these islands hardly a few tens of gerbil families (usually less) find room (fig. 8) and they do not form sufficiently independent groupings. Under such conditions originates a scarce non-sectionized settlement with a relatively uniform distribution of the gerbils.
The above-stated data permit us to conclude about the relation of the level of the population numbers of the gerbils and concerning the degree of its stability not so much from the absolute quantity and availability of food or from the favourableness of the sum total of other conditions, as from the population structure and from an interrelation of its component parts. This ecological flexibility of the population permits it to utilize the various territories, including those territories that are only suitable part of the time.

Non-differentiated populations originating in uniform (homogenous) or finely-mosaic landscape are unstable, because, as a rule, they are ensured with a lesser variation of fodders, shelters and other life conditions. Furthermore,
their structure contributes to spreading of infections
and to the activity of enemies.

Disjointed populations utilize diverse conditions,
while existance within them of relatively independent and
isolated (even temporarily) elementary populations makes
spreading of infections difficult, ensures a rapid resto-
ration of the numbers in a damaged grouping and presents
an opportunity by means of seasonal migrations and by means
of appearance of temporary elementary populations to utilise
a habitat more fully and many-sidedly. The cause of the
stability in the numbers of the entire ecological popula-
tion inhabiting the mosaic landscape consists in the inter-
action of the variegated elementary populations.

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Fig. 7. Fluctuations of the numbers of gerbils (percentage
of inhabited burrows) according to calculations in spring (B)
and in fall (O) in the "focus" of settlement (Otorbay) and on
its periphery (Karatyube) in the Uralian Karakums.
Arrows indicate destruction of rodents by poisons.
Evidently, the mosaic formation of the landscape only ensures the stability of population, when the dimensions of the mosaic elements are sufficient for the formation of independent elementary populations.

In other words, if the elements of the mosaic are equal or just slightly exceed the size of the individual or family section of the animals, the advantages of the mosaic formation of the landscape are lost to the rodents to a considerable degree. If the dimensions of the mosaic elements are hundreds or thousands times exceeding the dimensions of an individual section of an animal, then elementary populations originate.

Fig. 8. Scarce settlements upon the alluvial plane of Daryalyk-takyr.
1 - remnants of old river beds, 2 - sand islets with saxaul and sage, 3 - gerbil burrows.

At a further increase of the area each of the elements may become an independent biotope, and only along the narrow strip of its boundaries conditions for the stabilization of the numbers will originate.
Thus, the mosaic formation of the landscape, no matter of what type, is only an advantage at certain scales contributing to the stabilization of the numbers by means of sectionizing of the population. These scales are naturally not identical for different species and depend upon the character of their utilization of the territory and primarily upon the size of the individual sections. Therefore, even in the same species these scales may be different in different regions.

The discussed diagram explains satisfactorily also the differences in the stability of the numbers of different ecological populations. Among the latter one may segregate: temporarily, unstable and permanent, and stable populations.

At further migrations of animals, particularly in peak years of their numbers, the ecological populations are interconnected, same as the elementary populations are connected through the dispersion of the juveniles and through seasonal migrations. Therefore, the differences in the dynamics also of larger groupings - of geographical populations, may be explained by the interrelation between various types of ecological populations and the closeness of their connections. Indeed, all the Uralian Karakums and a portion of the northern Kyzylkums distinguish themselves by a relatively high and stable numbers of the gerbils, while the Daryalyktakyr flatland and the southern portion of the northern Kyzylkums have a less dense and less stable settlements. The northern
and the western Ural regions with their table and outlier relief and with the sands of the Bolshiye and Malyye Barsuki occupy an intermediate position.

Data known to us on other species of rodents support the above-discussed set-up. Thus, stable settlement of the water rat are restricted to the mosaic landscape of the Siberian forest-steppe (Maksimov, 1956). The same relation to a typical landscape is also known in the settlement dynamics of the field mouse (Frank, 1957; van Wijngaarden, 1957). In Germany and in Holland the field mouse is almost equally numerous both in regions where large plow-fields predominate, and in areas with a complex mosaic of small fields, hedges, boundaries, vegetable patches and coppices. But in the former mass multiplications alternate with depressions, while in the latter - there are no considerable fluctuations in the numbers of the field mice.

These factors require close attention to the study of spacial structure in the populations, of the inter- and intra-populational relations. Here one should not forget the existence of a special microstructure established by K. Petrusiewicz (1957; 1963). The knowledge and calculation of all this will increase considerably our possibilities not merely of making prognoses, but also to manage the dynamics of the populations.
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