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SPATIAL STRUCTURE OF MOUNTAIN POPULATIONS OF WOODLAND VOLES

O. F. Sadykov, V. N. Bol'shakov, and A. V. Bazhenov UDC 591.523

Results are presented of a complex investigation of the spatial structure of populations of woodland voles in the Ural Mountains. It is shown that during a large part of the year, the spatial structure is patchy, and the location of stable colonies (reservations)* does not change from year to year. It was established by tagging that voles living in local reservations widely utilize food resources of surrounding habitats and thus move away from nesting sites by hundreds of meters. In the course of a breeding season, there is an increase in the area of sites colonized, and thus those leaving a reservation with an area of 1-6 ha colonize an area of 400-1500 ha.

The spatial-temporal continuum of biogeocenoses at the populational level of organization breaks down into an ecological patchiness, the elements of which are utilized differentially by different species and intrapopulational groupings. As a patchy environment, following Wiens we understand an organism-determined spatial-temporal heterogeneity of the environment of specific organisms or their groups which is perceived by them more rapidly and reliably than is perceived by the investigator (Wiens, 1976). Ecological factors affecting populations display discontinuity in many spatial and temporal measures, and form a specific ecological patchiness of the environment of particular populations. Patchiness of the environment can be regarded as a matrix governing the ecological structure of a population and its adaptive reorganization. An important consequence of a patchy environment is a vrying dynamic of demographic processes in different structural subdivisions of a single population. With pronounced patchiness of the environment, differential utilization of living space becomes for short periods of time the most important element in the adaptive strategy of mobile organisms.

When studying the population dynamics of small mammals, the area actually covered by record keeping usually does not exceed 3 ha, and results obtained are then often extrapolated to a population as a whole, which is known to occupy a territory a hundred times larger. The postulate always at the basis of classical methods of estimation is not even mentioned; it assumes equal distribution of animals studied in the space to which data of estimates are extrapolated. However, in actuality, equal distribution of mammals in space is probably the exception, rather than the rule. Nevertheless, data of fragmentary records, summarized over a number of years, are at the basis of current concepts concerning dynamics of numbers and structure of populations of small mammals.

Estimation of populational parameters which consider features of the spatial structure of a population being investigated permits the level of our knowledge to be raised concerning the populational level of the organization of life, and the existing gap between a theoretical model of a population and the actual objects of empirical investigation to be reduced.

In order to determine whether an object of investigation conforms to the population level of organization, the position of S. S. Shvarts (1969) has important methodological value: that a population in the strict sense of the word is a set of micropopulations associated with one another by a commonality of origin from populational habitats of the reservation. It is simultaneously necessary to remember that a population is a potentially immortal structure, differing in this regard from any temporal groupings. Therefore, in structure the populational level of organization can correspond only to that spatial grouping of

*Translator's insertion.

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a species being investigated which occupies a space including a minimum of one reservation and the temporarily utilized, basic elements of the ecological mosaic adjacent to it.

The theoretical concepts presented above were at the basis of work conducted in 1978-1983 to study mountain populations of woodland voles. In mountains the altitude zoning and diversity of patchy landscapes create the objective prerequisites for the formation of complex spatial differentiation of animals. Small mammals are especially sensitive to environmental heterogeneity. For this reason reactions of populations in mountains to patchiness are more important than intrapopulational processes (Wiens, 1976). Woodland voles, the dominant group of rodents in the Ural Mountains, are the most convenient object for studying populational reactions of animals to patchiness of the environment, which are manifested first of all in features of their spatial structure.

Base work was conducted in 1978-1983 in the area of the high-altitude Iremel' massif (Beloretskii region of the Bashkir ASSR, 1586 m above sea level). Four to nine lines of 100 traps each were set at the same time at intervals of 10 m, usually for no more than four days. Pieces of Porolon impregnated with sunflower oil were used as bait. Permanent numbers were attached to all traps and the point of each capture fixed. Maps at a scale of 1:25,000 were used as the topographic basis when mapping. A total of more than 100 thousand trap-days were spent and more than 18 thousand small mammals were trapped, a large part of which were woodland voles of the genus *Clethrionomys*: red, red-gray, and bank.

The features of the assimilation of various elements of the ecological mosaic by animals were studied by tagging the animals, which was done in several ways: amputation of toes using a numbered code; bait stained with rhodamine-S and -6G dyes (Berdyugin and Sadykov, 1981); dye with ^{22}Na, ^{32}P, ^{35}S, ^{45}Ca, ^{59}Fe, ^{60}Co, ^{65}Zn, ^{89}Sr, ^{90}Sr, or ^{131}I radionuclides in doses of $3.7 \cdot 10^3$-$1.8 \cdot 10^5$ Bq at each baiting point (from 400 to 1500 such points fell within the area of tagging); subcutaneous injection during the entire breeding period of osteotropic calcium or strontium isotopes to mature females in order to obtain tagged young from them (Bazhenov, et al., 1983).

There were 45,800 trap-days directly in the tagging zones and 6,492 woodland voles were trapped, of which 704 were tagged with radionuclides and 102 with dyes. This permitted detailed analysis of the spatial distribution of woodland voles on four connected areas of 400 ha each and study of their territorial associations within the limits of 22 tagging areas measuring 10 to 200 ha and more. Basic attention was given to identifying reservations, tagging their inhabitants, studying the export of tags beyond the limits of the reservations, and a comparative study of the role of individual elements of the ecological mosaic and the work of ecotones characteristic for the region in the life of woodland voles. Results were used, in part, of work conducted along with I. L. Kulikova in 1981 in the northern Ural region where tagging with radionuclide yielded 364 animals on three parcels.

A large part of the experiments were conducted within the limits of the upper taiga subzone of the mountain-forest zone, and in the subpeak and mountain-tundra zones in the altitude interval of 900 to 1500 m above sea level. As a result of the significant elevation, climatic conditions in the area of base work contrast sharply with the climate of a large part of the southern Ural region. The average yearly temperature does not exceed -4°C, and the frost-free period lasts from 28 to 60 days in different years. The last snowfalls leading to temporary establishment of a snow cover were observed by us in the middle of June, and the first at the end of July-beginning of August. Phenomena catastrophic for small mammals, such as the formation of thick ice, slick ice crusts, and broad zones of flooding are regularly repeated in the mountains of the southern Ural region, especially in upper altitude zones.

In the course of surveying and selective trapping during periods of high water and the formation of solid ice, zones of woodland vole concentration were identified and mapped in the area of the Iremel' massif, which occupies approximately 400 km^2. Accumulations of woodland voles in such conditions turned out basically to be confined to rock detritus located on steep slopes and bordered by plant associations typical of each altitude zone. In the mountain-tundra band, the proportion of colonized areas during critical periods and unfavorable years constituted no more than one percent of the entire territory. In the sub-peak band, where rock detritus is the most extensive, the proportion of colonized areas constituted 10%, and approximately 5% in the mountain-forest band. During favorable periods of the year, no more than 20% of the territory was usually colonized at the end of the breeding season in mountain tundras, and up to 80% in the subpeak and mountain-forest bands.

The average numbers in summer during the years of observation on Mt. Iremel' fluctuated from 0.1 to 7% of voles trapped, while the number trapped in reservation always exceeded the average level for the mountain by many times and varied during the summer within the limits of 30-60%. The high level was also maintained in reservations during the autumn-winter period when woodland voles were almost absent on a large part of the area of mountain slopes. The year-round isolation of zones of high density of the woodland vole population in unfavorable years and the invariability of their spatial localization permitted us (Sadykov, 1980) to arrive at a conclusion about the possible maintenance of a patchy type of spatial structure in populations of red, red-gray, and bank voles.

The prolonged observations confirmed that reservations form a network of permanent reference points for mountain populations of woodland voles. Regular repetition of weather phenomena catastrophic for small mammals impedes the formation of stable colonies beyond the limits of rock detritus. The location of detritus colonized by voles and the structure of their deep layers eliminate the possibility of flooding by melting snow or torrential rains, and solid ice can not form on their surface. Numerous spaces between rocks, a surface layer of lichen, bryophytes, beds of turf-grass, bushes, and tree vegetation, the highly stable temperatures and humidity in deep layers of detritus, where the extremes of fluctuations of these very important abiotic parameters of the environment is two or more times less than on the surface (Berdyugin, 1979), make areas of detritus convenient habitats for many species of small mammals.

The majority of reservations studied by us are jointly used by three species of woodland voles. In 1979 we analyzed cases of successive catches of voles in the same trap in areas of the reservation of the three species. There were 378 cases of successive trappings of voles, including 100 cases when the capture of a red vole was followed by the trapping of a red, the trapping of a red-gray followed the capture of a red-gray in 81 cases, and of a bank by a bank in 89 cases. Red and red-gray voles were trapped simultaneously 57 times, red and bank 39 times, and red-gray and bank 12 times. There were no cases of joint trapping of females which had hibernated, which attests to their territoriality. On the whole, a species specificity can be discussed for a large number of migration paths of voles within the limits of jointly used reservations.

The tagging of inhabitants of reservations with dyes (Berdyugin and Sadykov, 1981) during critical periods showed that in winter voles do not travel more than 100 m from detritus and are usually satisfied with going to the closest edge for food. For this, they make use of common tunnels under the snow (Sadykov, 1978). With the appearance of the first thawed patches, voles begin to go 200-300 m beyond the detritus and 500-600 m after the snow is gone.

After the appearance of the younger generation, the settlement of mature animals from that year's birth is observed, depending on weather conditions, within the limits of zones of the regular feeding paths of the reservation's inhabitants, and breeding continues both in reservations and in the temporary colonies. If weather conditions are unfavorable, the new animals continue to live in reservations, but breeding stops. In the summer inhabitants of reservations extensively utilize food resources of rock-free habitats, independently of weather conditions. Using radioactive tagging, it was established that voles converting to an independent way of life travel far beyond the limits of the detritus for food (up to 1500 m and often 500-800 m). The combined use of three different radio-nuclides (^{89}Sr, ^{45}Ca, ^{65}Zn) and the trapping of 248 animals for comparative study of the utilization by woodland voles of food resources in areas of detritus, clearings, and mountain taiga showed that red and red-gray voles primarily feed in taiga habitats and obviously avoid clearings. Bank voles, on the other hand, feed primarily in clearings. The importance of areas of detritus for their inhabitants is insignificant in the summer: For each animal feeding in areas of detritus, there are 30 feeding at a distance of not less than 400 m from them.

The distribution of radioactive bait in various types of habitats showed that movement of woodland voles occurs primarily down various ecotones and along flood plains of mountain streams. Such distribution of bait permits animals to be noted which live on an area many times larger. For example, bait placed on 1 ha in a floodplain was detected during the next three days in 50% of 165 voles trapped on 200 ha.

Voles and other small mammals move especially intensively along floodplains of the largest mountain streams. It has been shown experimentally that during 24 hours radioactive label from a floodplain was detected in 90% of small mammals trapped within the same floodplain 1 km above or below along the course. The fastest straight-line movement of label by woodland voles, 1500 m in 24 hours, was established in areas with a developed network of stream floodplains.

Voles which lead a settled way of life according to data of capture in traps are well oriented toward sites distant by hundreds of meters from parcels of regular capture. This is also indicated by results of "homing" experiments. Red voles weighing 10-12 g, which were carried 300 m from the nest, returned to it during one night, while 24 hours was enough for mature animals to cover a distance of 1500 m. Therefore, it is not surprising that almost all voles living in detritus not only regularly leave its limits, but also make long journeys. It is important to note that estimates of daily movements of woodland voles, obtained on these slopes using repeated trapping, turn out to be different qualitatively, since according to this woodland voles move only 5-15 m per day (Berdyugin, 1980), i.e,, actual mobility of animals is understated by approximately two orders of magnitude.

In the course of three years, tagging of woodland voles was conducted within the limits of the same reservation with an area of 2 ha. At the end of the breeding season and with the start of the first snowfalls, trapping was conducted in temporary colonies 1 km away above and below along the slope. The reservation was in the subpeak, while the temporary colonies were in mountain tundra (upper) and mountain-forest (lower) bands. Trapping of more than 300 animals showed that in both temporary colonies all mature voles had a tag from the reservation. From year to year, settlement of voles proceeded along definite passages and bore an organized character.

Records kept showed that for a large part of the year, the spatial structure of the population of woodland voles in southern Ural mountains corresponds to a patchy type, with stable location from year to year of both permanent and temporary colonies. Only in favorable years is short-term transformation of spatial structure from patchy to diffuse noted at the end of the year (Fling, 1977) for red voles in subpeak and mountain-forest bands, and for bank voles only in clearings and in secondary forests of the mountain-forest band. For the red-gray vole spatial structure corresponds year-round to the patchy type because of the confinement of this species in the Urals to rocky habitats (Bol'shakov, 1972). In the mountain tundra band, the patchy type of spatial structure is maintained year-round for all species of woodland voles.

Such a usage of space by eurytopic species reflects an important side of the adaptive strategy of unspecialized species in unstable environmental conditions of the ecologic periphery of a geographic range, which the region of upper altitude bands undoubtedly is. The established spatial localization of stable basic colonies and their confinement to monotypic elements of the ecological mosaic attests to a rising tendency toward stenotopy in mountains at an altitude of 900 m and above.

The role of rock detritus for background species of mammals in the Ural Mountains is unusual. However, it should not be thought that all areas of detritus are equally suitable for the formation of stable colonies. Those which are located in intermountain basins and on gentle slopes are often completely unsuitable for colonization because of regular flooding. Areas of detritus are almost uncolonized which occupy the central parts of broad "rock seas." Woodland voles basically utilize the periphery of rock streams which are large in area, and their reservation is formed, as a rule, near highly productive rock-free habitats. The comparatively small primary productivity of areas of detritus is an additional reason for stabilization of vole density as compared to highly productive habitats. While increase in density of consumers in habitats with rich primary production is not limited by food resources until a "peak" in numbers and the direct undermining of available food associated with it are reached, the small-scale patchy plant associations of areas of detritus, which are low in productivity- are able to restrict growth in numbers of voles effectively and uniformly in periods when they are without other food sources. This is observed during unfavorable weather and between seasons when voles rarely leave the limits of detritus.

Surrounding the reservations, which are connecting elements in the spatial structure of populations, a zone is formed where inhabitants of the reservations go for food in the summer and where temporary colonies of incoming breeding voles develop. We call this second element in spatial structure the zone of a seasonal group regime of utilization. In addition, considerable areas in many bands fall within habitats where voles appear only in some periods and thus do not form colonies including mature and breeding individuals. We call this third element the reserve zone, since it can not be ruled out that in especially favorable years breeding of woodland voles will also occur here.

The complex combination of three separate zones on any specific parcel will also govern numbers and other populational parameters. In each zone distinguished, a particular course is observed for the dynamics of numbers and structure of the population, which is determined by the relationship of endogenous and exogenous mechanisms of population regulation operating in it. While exogenous factors play the chief role beyond the limits of reservations, restriction of numbers within them is associated with the operation of endogenous factors. However, since density of voles in reservations is usually associated with unfavorable weather conditions, endogenous mechanisms of regulation operating in reservations merely modify the influence of exogenous factors on the population, which transform the spatial structure of the population in such a way that realization of endogenous mechanisms of regulation is possible in theory. It is important to emphasize that in mountains, changes in spatial structure of populations always precede changes in their numbers, and the chief role of a specific ecological mosaic in the formation of any ecological populational structure is manifested.

What has been stated above permits a minimal grouping to be distinguished in space, the dynamics of which reflects on the whole the course of basic populational processes. In our opinion such a spatial grouping is one including the inhabitants of an individual reservation and settlements originating from it in zones of seasonal group utilization and in reserve zones. Judging by the capture of tagged voles in reservations, the overall area covered by such a grouping, which corresponds in structure to the populational level of organization, is from 4 to 16 km^2 for different species of woodland voles.

Such an approach to distinguishing minimal spatial groupings in natural conditions for any species of animal corresponding to the populational level is in complete agreement with the position of S. S. Shvarts (1969) mentioned above. It can be suggested that at the least, a true populations of woodland voles will be that spatial grouping which colonizes adjacent reservations and their periphery on a combined area with a radius equal to the maximal settlement of animals leaving these reservations during the entire cycle of population numbers, i.e., during two-four years, which can currently be determined experimentally. For objective estimation of basic populational parameters, it is enough to control a territory including one reservation as a minimum and all habitats within the radius of the maximal yearly settlement of young animals appearing in the reservation. Such a grouping can be called a micropopulation or subpopulation, since its structure basically corresponds to populational structure, although the territory occupied by it constitutes approximately 2.5-5.0% of the area of the population. The approach recommended by us to studying populational principles in woodland voles and other genera of small mammals similar to them in biology, therefore suggests the necessity of investigating the population of territories several hundred to several thousand hectares in area.

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