Ecological and Genetic Characteristics of the Distribution of *Bradybaena fruticum* Mull. (Mollusca, Gastropoda, Pulmonata) in a Forest–Steppe Landscape

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Abstract—The distribution pattern of the gastropod *Bradybaena fruticum* has been studied in a forest–steppe landscape. Analysis of the frequencies of polymorphic biochemical and conchological characters has yielded preliminary results on the characteristics of the species population structure whose formation was determined by a set of natural and anthropogenic factors.

INTRODUCTION

The study of populations of the terrestrial pulmonate *Bradybaena fruticum* (Mull.) that has been performed in the southern forest–steppe zone of the Central Russian Upland during the past seven years continues a series of large-scale studies on the population structure of this species, which is widespread throughout Europe. The goals of this study are (1) to estimate the effect of the natural geographic structure of the forest–steppe landscape on the spatial population structure of this species, which is characterized by a low mobility and, because of its ecological features, is confined to certain plant complexes and soils, and (2) to determine how the degree of anthropogenic landscape transformation affects the distribution of this species. Comparison of our data with the results of earlier studies performed in the northeastern part of the *B. fruticum* range (Matekin and Makeeva, 1977; Makeeva *et al.*, 1995; Batal' *et al.*, 1996; Khokhutkin, 1997) will contribute to knowledge of the vectors determining the dynamics of the species as a Mendelian population and of the gradients of factors in landscapes exposed to different degrees of anthropogenic impact.

MATERIAL AND METHODS

The mollusks were collected manually in summer. As a rule, several samples were taken from each colony. In each sample, we calculated the proportion of snails that had a longitudinal stripe on the shell ($S+$), which are considered to be homozygous for the corresponding recessive allele (Khokhutkin, 1979), and snails without the stripe ($S-$), as well as the frequencies of the most distinct color phenes of the shell: light yellow (C_3) and red-brown (C_1) in snails homozygous for the respective alleles. The shells of many snails were in different shades of light brown and pink (C_2). It was difficult to distinguish individual groups among them; hence, all these phenotypes were regarded as an inseparable mixture of heterozygotes at the alleles of light and red colors.

Two morphometric parameters, the width and the height of the shells of adult snails (in which the margins of the shell opening had formed a characteristic bend), were also analyzed. Several snails of each age were taken from each sample for electrophoretic analysis in polyacrylamide gel. The locus of the three-allele gene coding for one of monomeric esterases has been identified in *B. fruticum* (Matekin and Makeeva, 1977). The alleles of this locus (designated as *a, b,* and *c*) are inherited codominantly and, hence, yield six phenotypic variants. The data were processed statistically using the method of weighted means, calculation of variances, comparison of samples using Fisher's test (with significance of differences estimated by the ϕ method and by comparison of variances), calculation of genetic distances between populations, and Sjörensen's method. A total of 45 colonies from 20 sites were studied (Fig. 1). Conchological characters were analyzed in 6478 snails, and material from 2401 snails was studied electrophoretically.

RESULTS AND DISCUSSION

Humidity and temperature and, to a lesser degree, the characteristics of soil, relief, and vegetation are known to be the main factors affecting the distribution of terrestrial mollusks (Likharev and Rammel'meier, 1952). The specificity of these factors in the study region has determined the dispersal of *B. fruticum* in different elements of the forest–steppe landscape. This
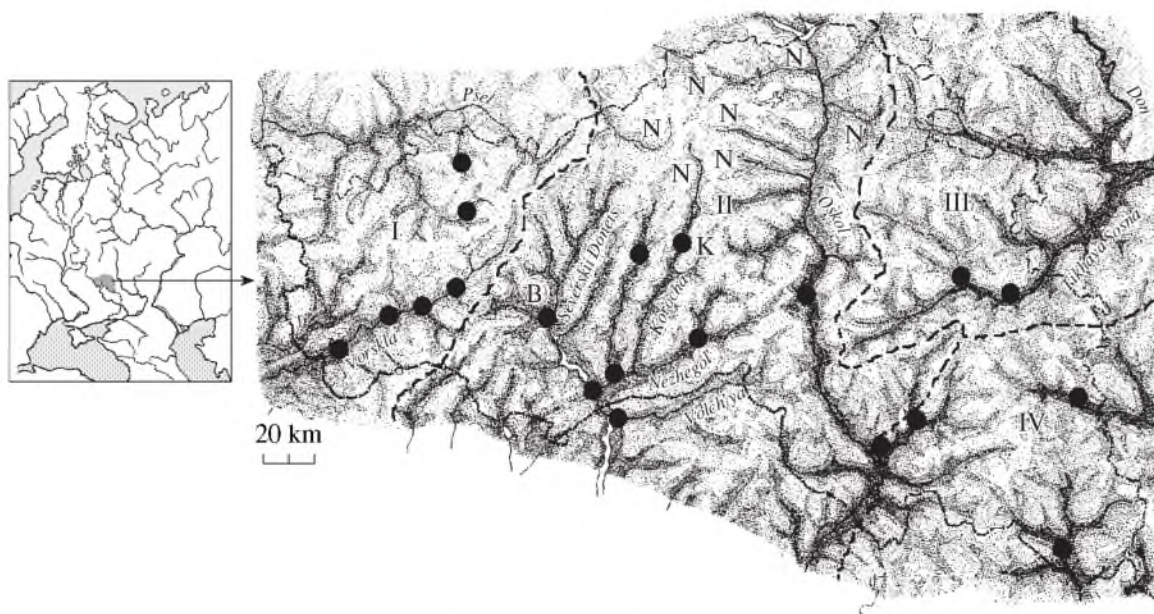
Fig. 1. Study region (according to Prisnyi, 1999). Solid circles show the sites of collection (B, Belgorod; K, Korocha; N, places where *B. fruticum* was absent). I–IV, PGRs and their boundaries: I, the Psel–Vorsklya PGR; II, the Oskol–Donets PGR; III, the Potudan'–Tikhaya Sosna PGR; IV, the Aidar PGR.

species is mesophilic; hence, as the climate in the southern part of the forest–steppe zone becomes increasingly arid, the snails concentrate in moist areas, such as floodplains and the bottoms of ravines and gullies. Thus, the range of *B. fruticum* habitats becomes narrower than in the northeastern part of the range, where these snails can live on watersheds. Today, only about 9% of the total area is suitable for *B. fruticum* in this region, which is incomparably smaller than in the northern parts of the range (around Moscow and Arkhangelsk and in the Cisural region, this proportion is 40, 51, and 44%, respectively).

Floodplain deciduous forests were the preferred habitats of *B. fruticum* in the study region. In addition, *B. fruticum* was often found in meadow communities and black alder forests, where the snails usually lived on elevations overgrown with nettle (*Urtica dioica*) or formed small aggregations at the periphery of the community. These snails were less frequent in floodplain and riparian oak forests. Their distribution in such biocenoses was usually restricted to clusters of burdock (*Arctium lappa*) or nettle in local depressions. In watershed and mountain oak forests and in steppes, *B. fruticum* was virtually absent. Sometimes, especially during rainy periods, a few age-1 snails were found in these areas. Age 1 is a dispersal stage, and these snails probably came from moist floodplain biotopes, attempting to colonize a new habitat. Apparently, such attempts were mostly fruitless, because neither older snails nor the shells of dead mature snails were found there. This agrees with the opinion (Khokhutkin, 1997) that snail migrations "are drastically limited during the reproductive period."

The distribution of *B. fruticum* was confined to certain biotopes within its habitats. These were usually willow or maple stands with tall herbaceous plants in the undergrowth, such as *Urtica dioica, Humulus lupulus, Arctium lappa, Heracleum sibiricum*, and *Angelica palustris*. Note that nettle was the main food of the snails in the study area, as it is in other parts of their geographic range; this nitrophilic plant grows in floodplains and low microlandscape elements naturally collecting surface runoff. However, climatic conditions of the southern forest–steppe affected the distribution of *B. fruticum* within the aforementioned plant associations. For example, during long droughts, which are usual in the study region, *B. fruticum* concentrated on the lower surface of large burdock leaves, which protected the snails from overheating. Large aggregations of *B. fruticum* of different ages were found during periods of drought in the axils and dead stems of *H. sibiricum* and *A. palustris*, where water was accumulated. In rainy periods, *B. fruticum* usually lived on *U. dioica* and *H. lupulus*. Experiments on food preference (Snegin, 2002) showed that the snails did not feed on *H. sibiricum* or *A. palustris* but used these plants as a shelter and a source of water. The same is indirectly confirmed by the fact that *B. fruticum* colonies formed in floodplain areas thickly overgrown with *A. lappa, U. dioica*, and *H. lupulus* (food objects) but lacking *H. sibiricum* and *A. palustris* were smaller than in the biotopes where all these plants occurred together. Such trends in distribution were not observed in the northeastern part of the *B. fruticum* range.

Small numbers of *B. fruticum* snails were found on poison hemlock, meadowsweet, motherwort, and

Fig. 2. A snail that has formed a false shell after injury.

marsh thistle. A few snails were found on tree trunks during heavy rains.

Morphometric parameters (shell width and height in adult snails) are good indicators of the effect of environmental conditions on these animals. These parameters strongly depend on air temperature and humidity, as well as on population density (Khokhutkin, 1971, 1997). In our study, the morphometric parameters were lowest in colonies located in black alder forests, waterlogged areas, and floodplain meadows, as well as in the driest steppe biotopes. In *B. fruticum* living there, the largest width and height of the shell were 17 and 14 mm, respectively. These parameters were higher (22 and 16.5 mm, respectively) in floodplains with a moderate moisture supply, with the population density being the same. Usually, these floodplains were covered with willow thickets, in which *A. lappa, H. lupulus, U. dioica*, and *H. sibiricum* formed an "understory." In one of these biotopes located in the Korocha River valley (Fig. 1, point K) at the bottom of a chalk slope with a southwestern exposure, we found a snail that had formed, after an injury, a "false" shell with a very narrow opening that did not allow it to withdraw into the shell during the drought (Fig. 2). The fact that this snail had nevertheless reached maturity also indirectly confirms that the biotope was favorable for *B. fruticum*.

The absence of *B. fruticum* from the northwestern and northern parts of the range, where average elevations above sea level are almost 50 m higher than in the study region (Fig. 1), may be explained by the effects of unfavorable factors, such as excessively high floods in the narrow riverhead floodplains, the absence of floodplain forests, river sources drying in droughty years, and the washout of substances rich in organic matter.

When analyzing the species distribution, we took into account the historical aspect. When the modern forest–steppe landscape had been formed in the postglacial period, *B. fruticum* apparently spread to this region along river valleys. Watersheds, which were absolutely unsuitable for meso- and psychrophilic mollusks because of the lack of water, served as natural isolating barriers, as they do now. It seems improbable that the snails spread to watershed areas in the past; the transformation of vegetation and soil that occurred then on watersheds is most likely to have been caused by the high intensity of geomorphological processes in the Central Russian Upland, rather than climatic changes (Mil'kov, 1950). Note that, while the river (its flood currents) may have been the main factor of the downstream dispersal of *B. fruticum*, the snails could only spread upstream travelling by land themselves. Their dispersal by birds, if any, could be only insignificant (this was only possible for young snails). Therefore, any unfavorable factor in the floodplain (an excessively high flood, sandy or swampy soil, etc.) must have restricted the dispersal considerably.

When studying such phenomena, the factor of time should be taken into account. If the "unfavorable" areas appear after the snails have spread throughout the floodplain, the range is naturally broken into half-isolated colonies. If the barrier has appeared in the process

of dispersal, then *B. fruticum* is absent in suitable biotopes upstream of the "unfavorable" area but often forms numerous colonies in similar biotopes downstream from it. We observed this phenomenon in the floodplains of the Korocha, Oskol, Nezhegol', Donetskaya Seimitsa, Oskolets, Khalan', Orlik, and Erik rivers. For example, *B. fruticum* is common in the Korocha floodplain; however, conditions for this species in an upstream area about 20 km in length are unfavorable. The floodplain becomes very narrow, with steep slopes devoid of forest plants; the banks are always flooded after rains. In the riverhead area, the floodplain is wider, and numerous springs flow from ravines and gullies overgrown with willows and clusters of *A. lappa, U. dioica, H. lupulus,* and *H. sibiricum*; in other words, the conditions are favorable for *B. fruticum*. However, we found neither live *B. fruticum* nor empty shells that would have indicated the presence of the species in this region in the past. Note that another gastropod, *Succinea putris* (L.) (a constant "companion" of *B. fruticum*), which is a psychrophile and tolerates excessive moistening, was found both throughout the "unfavorable" area and near the riverhead. A similar situation was observed in the upper Nezhegol' basin. The analysis of species dispersal may shed light on the history of the processes that occurred in the floodplains of rivers flowing in the region studied.

Currently, not only natural conditions, but also human activities substantially affect the distribution of *B. fruticum* in the forest–steppe landscape. The forest–steppe of the Central Russian Upland is subjected to a heavy anthropogenic load (*Sostoyanie...*, 1999). Anthropogenic isolation adds to the natural isolation determined by the forest–steppe landscape. The natural species range has been excessively split because the land is intensely cultivated (as much as 80% of the area is plowed), the relief is markedly partitioned, the forested area is small (10%), and roads and dams have been built. The snail distribution is distinctly mosaic and almost entirely restricted to the remaining floodplain islets of willow and alder thickets, which makes it considerably easier to determine the boundaries of *B. fruticum* colonies. The distance between individual colonies in the regions most strongly affected by human activities varies from several hundreds of meters to 2–3 km. The unsuitability of the anthropogenically altered floodplain areas for *B. fruticum* is evidenced by the fact that the species was either entirely absent there or only age-1 snails (which are, as noted before, the dispersal stage) were found. The complete absence of adult (mature) snails (and even snails of age 2) indicates that *B. fruticum* is being eliminated in these areas. Mature snails were only found in a few remaining islets of favorable biotopes serving as centers of dispersal. In my opinion, this characteristic distribution pattern of the species has affected the genetic structure of its populations.

The genotypic analysis of the spatial structure of *B. fruticum* distribution based on the frequencies of *S*+

and *C*₃ alleles and phenes, as well as esterase gene alleles, demonstrated a high originality of most snail colonies that were located in different areas and isolated from one another. According to the observed mean frequencies and variances, most colonies studied (62%) should be considered to be separate populations in the strict, genetic sense. Other colonies were parts of subdivided populations (i.e., demes). If the formation of the populations is favored by natural isolation (swampy and sandy areas of the floodplain, chalky slopes, etc.), only the genetic diversity of divided groups is formed. If populations are isolated because of anthropogenic factors, the natural subdivision of the species is disturbed. In contrast to natural barriers, most artificial ones (roads, railway embankments, quarries, etc.) appear so rapidly that *B. fruticum* has not enough time to overcome them. This results in stronger isolation, genetic drift, and a decrease in population genotypic diversity, which we observed in several "anthropogenic" colonies. For example, in a small colony at the bottom of a ravine near the city of Belgorod (Fig. 1, point B), isolated because of the construction of brick works, 100% of snails were homozygous for esterase allele *b* and the frequencies of homozygous phenotypes *S*+ and *C*₃ (0.282 and 0.333, respectively) were increased compared to the original colony located in the floodplain of the Severskii Donets River (Fig. 3), where the frequencies of allele *b* and phenes *S*+ and *C*₃ were 0.835, 0.084, and 0.140, respectively (Fisher's test values (the ϕ method) were $F_{S+} = 7.2$, $F_{C_3} = 11.3$, and $F_b = 28.1$; the respective F_{St} values are 3.9, 6.8, and 11.2).

Although most colonies studied were true populations, their genotypic and allelic compositions were sufficiently similar to permit their uniting into population groups of the next level of distribution structure, which we termed *points*. A total of 20 such points were distinguished (Fig. 1). The comparison of population groups assigned to different points with respect to the concentration of alleles *S*+, *C*₃, and *b* (the most frequent esterase allele) showed that each group significantly differed from others in *S*+ allele frequency in 60% of cases. The degrees of isolation with respect to the *C*₃ and *b* allele concentrations were estimated as 45 and 43%, respectively. The comparison of variances with respect to these alleles showed an even larger isolation of the points. The groups compared belonged to different general populations with respect to alleles *S*+, *C*₃, and *b* in 89, 94, and 87% of cases, respectively, which was accounted for by two factors. First, the specific geomorphological and microclimatic conditions of each point served as factors of natural selection; second (which could be more important), the points were separated from one another by anthropogenically altered parts of the landscape unsuitable for *B. fruticum*.

The comparison of the *B. fruticum* population structure in the southern part of the range and in the Moscow region, where this structure has been studied in most detail (Batal', 1996), showed a more structured spatial population pattern of its distribution (i.e., more cases of
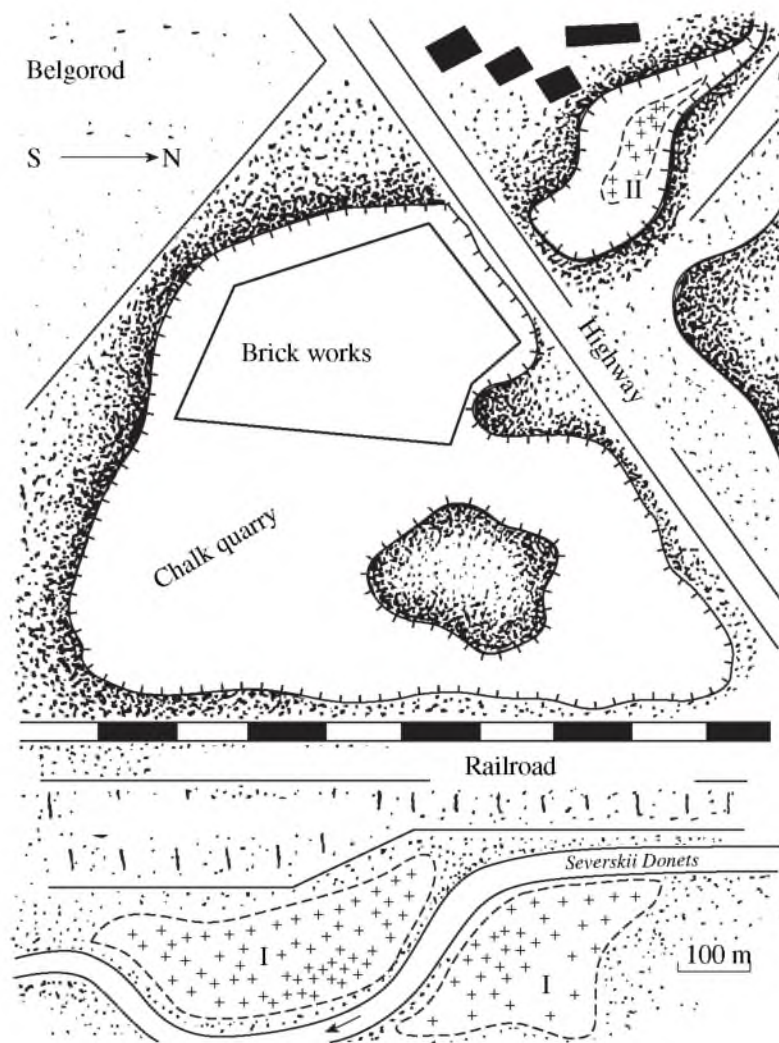
Fig. 3. Colonies of *B. fruticum*: (I) original and (II) isolated.

significant differences between colonies) in the southern part of the forest–steppe zone, because the species range was more partitioned there.

On the other hand, similar characteristics of abiotic factors in points belonging to the same of the four physiographic regions (PGRs) that may be distinguished in the total region studied (Chendev, 1996; Fig. 1) made it possible to unite these points into the next hierarchical level of the species population structure, PGR population groups of points. The results of this study indicate that, as the climate becomes more continental in the direction west to east, the proportion of homozygous phenotypes ($S+$, C_3, and bb) in PGR population groups of points significantly increases (Fig. 4). Note that the easternmost Aidar PGR belongs to the steppe zone; in addition, it was radioactively contaminated after the Chernobyl accident. This should be taken into account when estimating the deviations of frequencies.

Regarding the total *B. fruticum* population of the southern forest–steppe, it is characterized by low pro-portions of snails with a longitudinal stripe on the shell (0.133) and with yellow shells (0.108). Phenes $S-$, C_2, and C_1 are most prevalent in *B. fruticum* populations in this region (0.867, 0.662, and 0.230, respectively). Esterase allele b is the most frequent (the mean frequency is 0.8). In most populations, this allele is present in a homozygous form (bb; mean frequency, 0.7). The other alleles (a and c) are substantially less frequent (0.086 and 0.114, respectively).

Thus, the analysis of phene and allele frequencies in populations, points, PGRs, and the total population has made it possible to reveal the hierarchy of the *B. fruticum* population structure in the southern forest–steppe, which is largely determined by the gradients of natural factors. However, this relationship is often distorted, because the genotypic characteristics of some populations and their groups do not fit this hierarchical structure. This is expressed as an unexpected increase or decrease in the frequencies of some alleles and phenes
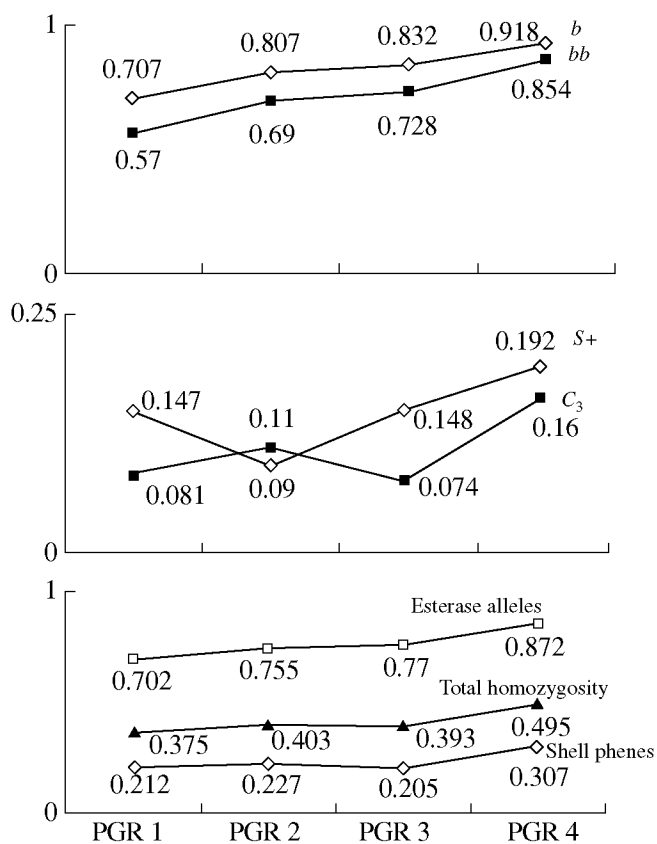
Fig. 4. Clinal changes in allele and phene frequencies in *B. fruticum* populations of different PGRs.

because of genetic drift determined by anthropogenic factors in individual populations.

Collating the results of this study with the data obtained in the northeastern part of the species range, namely, the Moscow, Arkhangelsk, and Yekaterinburg regions (Batal' *et al.*, 1996), we obtain the following general pattern. The *S*+ phene frequency exhibits a clearly clinal variation, namely, a significant northward increase in the proportion of striped snails (0.133, 0.411, 0.412, and 0.712 in the Belgorod, Moscow, Yekaterinburg, and Arkhangelsk regions, respectively). This clinal change in the population frequency of striped snails confirms experimental data on the higher survival rate of young *B. fruticum* without stripes at increased temperatures (Matekin and Makeeva, 1979). There are also data (Runkova *et al.*, 1974; Khokhutkin 1976) on the greater energetics of striped snails, in which increased oxidative enzyme activity at lower temperatures enables the animals to adapt to cold at the least energy cost possible.

Phene C_3 (a yellow shell) is under the pressure of natural selection in all parts of the species range, and its values are always low (0.109, 0.108, 0.2, and 0.176 in the Arkhangelsk, Belgorod, Moscow, and Yekaterinburg regions, respectively). In the Arkhangelsk and Moscow regions, as well as in the southern forest–

steppe, esterase allele *b* was the most frequent (0.775 and 0.561, respectively), and its transition to a homozygous state was observed in both regions. In the Yekaterinburg region, the proportions of alleles *c* and *a* were drastically increased (0.672 and 0.224, respectively). This may have resulted from increase in the polymorphism of nettle, the main food of *B. fruticum*.

In addition to the aforementioned approaches to studying the phenotypic structure of populations at different levels of hierarchical complexes, we also analyzed the frequencies of combined phenotypes. These were the combinations of one of the three shell-color phenes, the phene of the presence or absence of the stripe, and one of the six esterase phenes. All age groups were analyzed. We found 33 out of 36 possible combinations. The number of combinations was decreased in steppe, swampy, and anthropogenically altered biotopes. In the former two cases, there was intense selection for the combinations best adapted to conditions unfavorable for the species; in the latter case, the decrease in gene-pool diversity was related to inbreeding.

We also estimated two more parameters, the spread of the combined phenotypes (the percentage of populations where the given phenotype was found) and their abundance (the proportion of snails with the given phenotype in a population or a population group). All combinations were arbitrarily divided into groups that we termed *prosperous*, *depressed*, *discriminated*, and *absent*. The prosperous combined phenotypes had a mean abundance of at least 0.15 and a mean spread of at least 80% in the total region studied. There were only two of these phenotypes, C_2S– *bb* and C_1S– *bb*. All other combinations were considerably rarer. The depressed phenotypes had an abundance higher than 0.05 and a spread of 50–70%. Almost all of the corresponding genotypes contained allele *b*. These were C_1S+bb, C_2S+ *bb*, C_2S– *cc*, C_2S– *ab*, C_2S– *bc*, and C_3S–*bb*. The discriminated phenotypes had an abundance no more than 0.05 and a spread less than 50%. In addition, the combinations that were found only in the young and had low frequencies were included into this group. Most snails from the "discriminated" group had esterase alleles *a* and/or *c*. This group included almost all remaining combinations (26). The group of absent phenotypes included combinations that were theoretically possible but were absent in all samples and at all ages. All snails in this group had a stripe on the shell and contained esterase allele *a*; there were three such phenotypes: C_2S+ *aa*, C_3S+ *aa*, and C_3S+ *ac*.

Some of the combined phenotypes that were discriminated or depressed in the southern forest–steppe as a whole were prosperous in some individual colonies, and vice versa. This indicates different directions of natural selection under different conditions.

According to the results of earlier studies (Batal' *et al.*, 1996), most of the combined phenotypes in the northeastern part of the range were prosperous (5) or
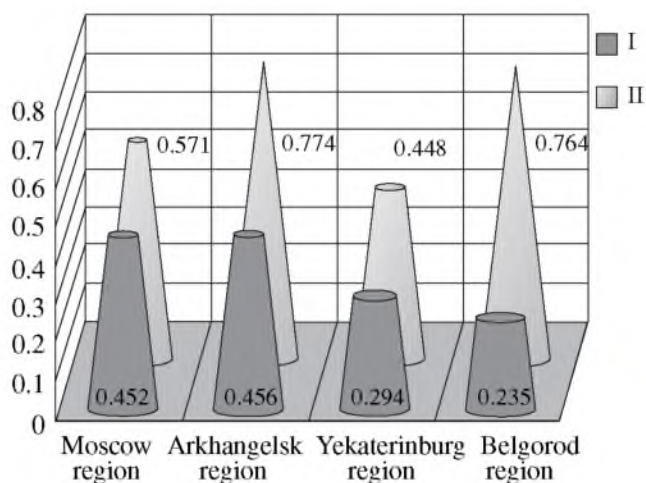
Fig. 5. Population homozygosities with respect to (I) shell phenotypes and (II) esterase alleles in different parts of the species range.

division of a species based on the polymorphism of genomic loci favors the species survival in space and time.

Note that the data obtained also make it possible to differentiate between the natural population structure and the population subdivision caused by anthropogenic factors. In the latter case, random genetic drift in isolated populations may lead to a ratio between allele frequencies that will considerably decrease the population survivability and form conditions extremely unfavorable for the species in the long term. Unfortunately, not only the species studied, but also the entire biocenosis of the southern forest–steppe faces this hazard.

depressed (25). Our comparison demonstrated a distinct trend towards a decreased diversity of combined phenotypes in the southern group of populations, because most of these phenotypes are discriminated (in the northeastern part of the range, only six discriminated phenotypes have been found).

In some cases, anthropogenic impact accelerates the decrease in population genotypic diversity because of the large amount of homozygous snails (Lewontin, 1974). The results obtained demonstrate high homozygosity in all parts of the range with respect to both the esterase locus and the genes determining shell phenotypes (Fig. 5). In three regions, the increase in population homozygosity resulted from the high frequency of esterase allele b (in the Yekaterinburg region, allele c). Note that, since the food object was stable, the homozygosity for the esterase locus reflects isolation and the resultant genetic drift to a higher degree than the homozygosity for the loci determining the shell phenes, which has resulted from natural selection. Certainly, the transition of an allele into a homozygous state may be physiologically optimal for an individual or population but only for a narrow range of environmental conditions. A small change in these conditions may be catastrophic because of the decrease in fitness. Therefore, homozygotization is both useful and hazardous, with unbalanced, accidentally formed "anthropogenic" populations being especially endangered.

The comparison of the mean frequencies of alleles $S+$, C_3, and b in the total southern group of populations in different years has shown only insignificant differences. This temporal stability indicates that, in general, the southern populations can maintain a certain level of hereditary variation. This confirms the theory developed by Chetverikov (1926), Altukhov (1995), and other scientists according to which the population sub-

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