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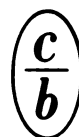
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DIFFERENTIATION OF A POPULATION OF FIELD MICE (*Apodemus agrarius* PALL.)
IN AN URBANIZED AREA

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Study and comparison of the morphometric and phenetic differences of five isolated colonies of field mice indicated that a population of this species in the city is separated into intraspecific groups that are, in a number of cases, well-differentiated populations. The specifics of each of the groups are related to a different origin and to the effect of anthropogenic factors, most importantly those which reinforce the isolation of the groups. A theoretical view of the formation of the urban colonies of the studied species is considered.

It is known that several different rodent populations can coexist in a very small area in cities (Lisin and Petrov, 1982; Andrzejewski et al., 1978; Babinska-Werka et al., 1979, 1981; Sikorski, 1982; and others). The formation of these populations occurs after the inclusion of part of a settlement of natural populations within the limits of a growing city. Due to human activity, they exist under conditions of increasing isolation relative to similar groups and exurban colonies. In a city, it is easily possible in a majority of cases to determine the duration of autonomous existence and the spatial limits of rodent groups. Development of these groups is closely connected to the features of construction of those areas of the city in which their habitats are located. Having studied and compared individual rodent populations within the boundaries of a city, we are approaching a real solution to the problem of determining the mechanisms of the origin and the independent existence of such colonies in an urbanized area.

The goal of the present work is to reveal the degree of morphological differentiation of urban groups of the field mouse (*Apodemus agrarius* Pall.) relative to one another and, on the basis of the collected morphometric and phenetic data, to attempt to reconstruct a picture of the formation of the studied colonies of this species in the city of Gorky.

In 1979-1981 (from May to October) in the city of Gorky, 2073 field mice were captured using standard trap-line methods (a total of 10,750 trap-days was worked). Five groups of this species were identified; morphological features were also studied in samples of these groups. All the criteria applicable to a population were formally applied to each group, although we consciously limit ourselves in their description to the neutral terms "colony" and "group."

Age of the animals was determined by the degree of wear on the molars and by the condition of the pelage (Varshavskii and Krylova, 1948; Haitlinger, 1962; and others). For analysis of morphometric characters, data from three years were combined. Because of the large volume of material, we limited ourselves to some data on males of the older age group (older than 8 months), which were captured each year in June-July (see Fig. 3).

The degree of phenetic differentiation of the separate rodent groups was determined on the basis of study of a complex of nonmetric threshold skull characters using the method proposed by Berry (1963). The effectiveness of this method for the indirect exposition

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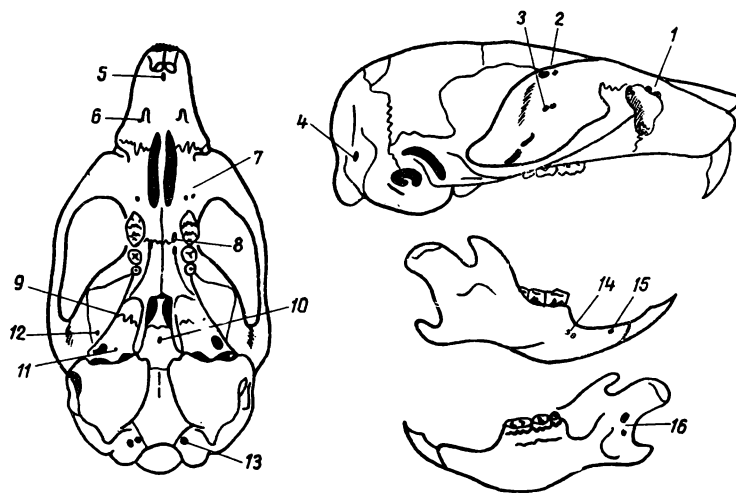


Fig. 1. Location of nonmetric characters on the skull of the field mouse: numbers 1-16 correspond to the numbers of the characters in the text.

TABLE 1. Frequency of Occurrences of Nonmetric Characters in the Field Mouse Skull in Urban Colonies

No. of character	Colonies									
	Bugrovskoe		Shchelokovskoe		Priokskoe		Shuvalovskoe		Avtozavodskoe	
	P/N	%	P/N	%	P/N	%	P/N	%	P/N	%
1	4/84	4,8	11/208	5,3	2/62	3,2	0/72	0	3/122	2,5
2	64/84	76,2	147/212	69,3	40/62	64,5	28/76	36,8	100/125	80,0
3	37/84	44,0	114/212	53,8	41/62	66,1	41/76	53,9	70/125	56,0
4	72/72	100,0	159/162	98,1	40/42	95,2	55/56	98,2	80/90	88,9
5	27/42	64,3	76/103	73,8	23/31	74,2	35/36	97,2	52/60	86,7
6	12/84	14,3	47/208	22,3	6/62	9,8	30/74	40,5	44/121	36,4
7	49/84	58,3	120/210	57,1	27/62	43,5	49/76	64,5	59/125	47,2
8	9/84	10,7	28/211	13,3	6/62	9,7	13/76	17,1	13/125	10,4
9	9/78	11,5	31/184	16,8	5/52	9,6	2/64	3,1	2/106	1,9
10	30/41	73,2	59/92	64,1	13/26	50,0	24/32	75,0	30/48	62,5
11	64/82	78,0	159/188	84,6	40/54	74,1	58/64	90,6	63/103	61,2
12	47/81	58,0	124/188	66,0	31/54	57,4	26/63	41,3	65/101	64,4
13	52/71	73,2	127/157	80,9	31/40	77,5	46/54	85,2	61/87	70,1
14	69/84	82,1	132/217	60,8	45/63	71,4	51/75	68,0	83/128	64,8
15	39/84	46,4	105/216	48,6	32/63	50,8	44/75	58,7	81/128	63,3
16	3/84	3,6	53/216	24,5	5/61	8,2	19/75	25,3	21/126	16,7

Note. P is the number of individuals or sides of the skull of an individual bearing the characters; N is the total number of observations (for bilateral characters, the number of studied skull sides).

of the genetic differences between natural groups has been demonstrated in a number of works (Vasil'ev, 1982, 1984; Berry and Jakobson, 1975; Hartman, 1980; Sikorski, 1982). We studied 16 nonmetric skull characters that were not related to one another, or to the age or sex of the animals: 1) preorbital foramen divided; 2) frontal foramen divided; 3) ethmoid foramen divided; 4) prolapse of a fragment of the external mastoid part of the petrous temporal bone of the auditory bulla; 5) presence of a large "incisive" foramen on the premaxilla; 6) presence of a paraincise "fossa"; 7) supramaxillary foramen divided on the ventral surface of the supramaxilla; 8) large palatine foramen divided; 9) prolapse of a fragment of the palatine bone in the region of the palatopterosphenoid commissure; 10) presence of a medial foramen on the main sphenoid; 11) presence of an "innominate foramen; 12) presence of an additional foramen near the foramen ovale; 13) single foramen of the hypoglossal canal; 14) mental foramen divided; 15) presence of a subincisive foramen in the lower maxilla in the region of the diastema; 16) mandibular foramen divided.

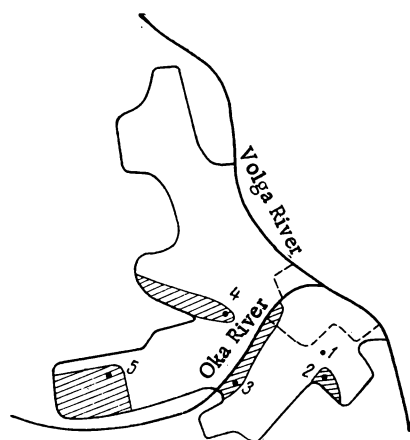


Fig. 2. Map of the locations of the capture areas (1-5). Zones of possible contact with rodents of the studied colonies are shaded. Boundaries of the city in 1916 are indicated by the dotted line.

The Russian names presented for the characters are preliminary and should be considered only as conditional working designations. Their locations are shown in Fig. 1, and their occurrence in the compared samples is presented in Table 1.

Due to the need for reliable classification of the characters, only individuals older than one month, captured in June-July, 1981, were compared in the phenetic evaluation. The index of differentiation (D) was calculated using the method described by Berry (1963):

$$D = \frac{1}{r} \sum_{i=1}^r \left[(\theta_{i1} - \theta_{i2})^2 - \left(\frac{1}{n_{i1}} + \frac{1}{n_{i2}} \right) \right], \quad (a)$$

where $\theta = \arcsin (1-2 p)$; p is the frequency of occurrence of a character in fractions of the whole; n_{i1} and n_{i2} are the number of observations of the i th character (for bilateral characters, the number of studied sides). Standard deviation was calculated by the formula proposed by Sjøvold (1973):

$$S = \frac{1}{r} \sqrt{\sum_{i=1}^r 2 \left(\frac{1}{n_{i1}} + \frac{1}{n_{i2}} \right)^2}, \quad (b)$$

where r is the number of studied characters.

The lower course of the Oka River, which is 650-700 m wide at low water level near its mouth within the city limits, divides Gorky into two parts differing in the character of their natural conditions: the high uplands, and the lowlands beyond the river. Three of the five study areas are located in the upland part of the city (1, 2, and 3), and two (4 and 5) in the river bottomlands (Fig. 2).

Area 1 is the grounds of the Bugrovskoe Cemetery (17 ha), which is located almost in the center of the upland section; it is enclosed by a stone wall and is surrounded on all sides by densely built-up apartment blocks. The cemetery was developed in 1914 outside the city limits, and was incorporated into the city in the 1920s.

Area 2 is the northern part of the cemetery in Mar'inaya Grove, which is located 2 km south of the previous sector on the city perimeter (the cemetery was developed in 1939). Areas 1 and 2 were connected until the 1920s by a continuous green tract of the Mar'inaya Grove, and the possibility of contact was subsequently maintained through empty lots and gardens. In the 1950s, after the creation of high-density apartment blocks, the isolation of the areas increased sharply.

Area 3 is located on the peak of the slope of the right main bank of the Oka River, 5 km southwest of the previous area. On the northwest, the slope drops steeply to the river; on the other sides, the area is bounded by a highway and apartment blocks. Until the 1940s, there was no barrier between Area 3 and the two previous areas, and they were isolated only

TABLE 2. Phenetic Distances (index of differentiation, D) between Urban Field Mouse Colonies (lower triangular matrix contains the standard deviations)

Colony	Bugrovskoe	Shchelokovskoe	Priokskoe	Shuvalovskoe	Avtozavodskoe
Bugrovskoe	—	0,046	0,028	0,179	0,102
Shchelokovskoe	0,007	—	0,026	0,106	0,066
Priokskoe	0,013	0,010	—	0,139	0,047
Shuvalovskoe	0,011	0,008	0,014	—	0,127
Avtozavodskoe	0,009	0,006	0,011	0,010	—

by distance. In the 1950s, when Area 3 was incorporated into the city, they were already practically unconnected.

Area 4 is located almost in the center of the river bottomlands, and is a marshy depression along the banks of the Shuvalovskoe Lakes. Densely built-up regions adjoin the lakes on three sides. The area was incorporated into the city in the late 1940s and early 1950s.

Area 5 is the southwest part of the Avtozavodskoe Cemetery, which is located 11 km southwest of the previous area. The cemetery was founded in 1938, at what was at that time a considerable distance from the city limits. The present peripheral position of this habitat maintains the possibility of wide contacts between its resident rodents and the population in the natural biotopes along the left bank of the Oka.

We will henceforth designate the field mouse population in the different areas in the following way: 1) the Bugrovskoe colony (group); 2) the Shchelokovskoe colony (the section of the Mar'inaya Grove adjoining the cemetery bears the name of Shchelokovskii Farmstead); 3) the Priokskoe colony; 4) the Shuvalovskoe colony; 5) the Avtozavodskoe colony.

Based on morphometric characters of the body and skull, the studied colonies are clearly divided into three groups: all the upland colonies, the Avtozavodskoe colony, and the Shuvalovskoe colony. The latter colony is especially sharply delineated. The diagram constructed from the mean values of three arbitrarily chosen morphometric characters, based on data from over-wintering males in the summer samples (three-dimensional coordinates), graphically illustrates the general degree of morphometric difference between the upland and riverbottom colonies (Fig. 3).

We will examine the obtained estimates of the phenetic differentiation of the individual groups. This is apparent in Table 2, where the colonies can also be divided into three groups: the first consists of the upland colonies, the second is the Shuvalovskoe colony, and the third is the Avtozavodskoe colony. Samples from the Bugrovskoe, Shchelokovskoe, and Priokskoe colonies are phenetically the closest. Formerly, before the construction of the part of the city in which these colonies are found, they apparently were united. Until the 1940s, they were not isolated, but, with expansion of the city limits, their isolation increased; by the early 1950s, they had become practically disconnected by areas of continuous masonry construction and ribbons of motorways. Thus, it can be assumed that the isolation reached its present level approximately three decades ago (which is equivalent to the succession of about 100 generations of the rodents). In the city, neighboring populations separated by even a small distance can be situated in different habitat conditions. In our case, the differences between the colonies depend on their position along a gradient from the perimeter of the city to its center: with increasing distance from the city limits, the degree of isolation from natural biotopes intensifies and the effect of anthropogenic pressure increases, eliciting an uneven response from the groups. The selective directions and pressures on the colonies may not coincide, which created the preconditions for their further differentiation.

Of interest among the three upland populations are the disproportionately large differences between the Bugrovskoe and Shchelokovskoe colonies, the two closest groups, which are undoubtedly connected with the strong isolation and specific living conditions of the Bugrovskoe group. Sikorski (1982), conducting an analogous study of urban field mouse populations in Warsaw, obtained estimates of phenetic distances close to ours (in his terminology the mean measure of divergence). For different pairs of compared colonies (in his view,

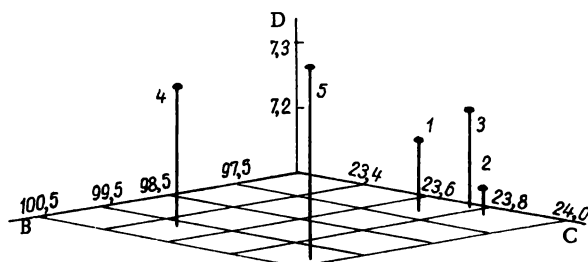


Fig. 3. Comparison of field mouse colonies by morphometric characters. Colonies: 1) Bugrovskoe; 2) Shchelokovskoe; 3) Priokskoe; 4) Shuvalovskoe; 5) Avtozavodskoe. D) diastema length, mm; B) body length, mm; C) condylobasal length, mm.

populations), the value of the index of differentiation fluctuated between 0.011 and 0.056, making it possible to speak of genetic differentiation within the city limits. Our data on the closely neighboring colonies in the upland area are also convincing on this point.

The Avtozavodskoe colony differs significantly from the Bugrovskoe and Shchelokovskoe groups, but is close to the Priokskoe colony, which is sort of a border group between these two aggregates. Judging by the low level of phenetic differences, contact occurs between the Avtozavodskoe and Priokskoe colonies, despite the fact that they are located on different sides of the Oka floodplain. The possibilities of settlement along and through river valleys by even less mobile rodent species have been well demonstrated by A. A. Maksimov (1974). Considering the direct connection of both groups with the natural biotopes along the Oka floodplain, it can be assumed that the similarity of these two colonies stems from just such a basis.

The Shuvalovskoe colony differs significantly from all the others. The differences are so substantial that it can confidently be described as distinct. The value of the index of phenetic differentiation cannot be considered to be an absolute measure of differences, but, as a relative quantitative measure, this index is universally applicable for comparison of populations within various species. The level of differences found in this case agrees with that generally observed between significantly differentiated populations of other species (Vasil'ev, 1982; Berry and Jakobson, 1975; Hartman, 1980).

Of interest in this scheme is the high level of differentiation of the Shuvalovskoe and Avtozavodskoe colonies, which are located in the riverbottom section of the city. The distance between them is comparatively small, 11 km; they have been completely separated since the 1950s, that is, approximately as long as have the Bugrovskoe and Shchelokovskoe groups in the upland section. If it is assumed that they composed a single population aggregate before the construction of that section of the city, then it is impossible to explain such an order of differences (see Table 2), three times greater than in the case of the upland groups, one of which is completely isolated. Obviously, this is a matter, not so much of the progressive isolation of the riverbottom colonies, but of their initial genetic variability. In our view, this group is connected in its origin and existence to the population complex along the Volga floodplain. At present, the possibility of contact between this colony and the natural biotopes along the Volga is unlikely, considering the increased urbanization of this area. A hypothetical scheme of the connections of the urban field mouse colonies is presented in Fig. 4.

On the basis of our phenetic and morphometric data, an attempt can be made to reconstruct a picture of the formation of the studied colonies. Originally, in the riverbottom area before the construction of the city within its present limits, the field mice formed two population complexes: the Volga complex along the Volga River; and the Oka complex, which today is in the southern section of the city connected with the floodplain of the Oka. The possibility of contacts between them was greater at that time than now, and they apparently differed less. The third complex inhabited the upland area and obviously was strongly influenced on the Priokskoe Slope by the Oka group (first, due to contacts; second, possibly due to a similar origin of these complexes) and, closer to the Volga River, by the Volga group. The construction of the city, the emergence of powerful isolating factors, and the appearance of multidirectional anthropogenic factors led to a further differentiation of

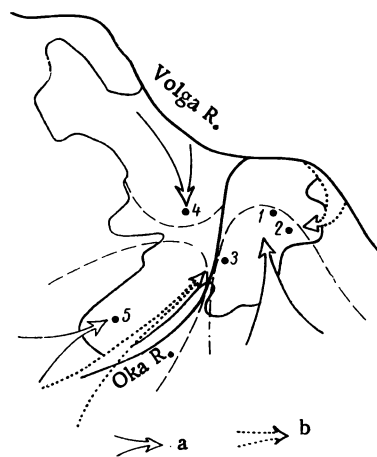


Fig. 4. Scheme of the possible connections of the field mouse colonies. Boundaries of the probable original population aggregates are indicated by the dashed lines. Arrows) the routes of direct (a) and indirect (b) influence from natural populations; 1-5) see Fig. 3.

the remaining colonies. The contacts between the Avtozavodskoe and Shuvalovskoe colonies were disrupted. Delimitation of the upland colonies led to a severe weakening of the connection of the Priokskoe with the Bugrovskoe and Shchelokovskoe colonies, and, through these, also with the Volga group, and, consequently, a relative increase in the connection with the Oka population complex, especially with the Avtozavodskoe colony. The Bugrovskoe colony began to develop independently from the Shchelokovskoe, which continues to be influenced by the Volga group. Consequently, the differentiation of the upland populations was furthered, along with increasing isolation, and the influence from various population aggregates increased relatively.

The morphometric and phenetic specifics of each population group have, in our opinion, two causes. The first of these is the different origin of the groups. The deepest difference is established between the river bottom and upland colonies; the two riverbottom groups also differ significantly from one another. It is possible to distinguish at least three large colonies, the differentiation between which is due to the fact that, before inclusion within the city limits, they apparently embodied different population complexes existing to a greater or lesser degree in isolation. The second cause is found in the differentiation of the colonies due to anthropogenic factors. Important roles are played by the increase in degree of isolation and the specifics of ecological conditions of each of the habitats. This is obviously also connected with the isolation of several colonies in the upland population.

Thus, the field mouse population in the city is divided into intraspecific groups differing substantially from one another in a number of studied characters. The similarity of the data obtained from the study of morphometric and phenetic characters makes it possible to confidently describe the Avtozavodskoe and Shuvalovskoe colonies as belonging to two differentiated populations. The differences between the separate upland field mouse colonies do not, in our opinion, attain "good" population level, although their distribution in itself and the long term of autonomous existence are evidence that we are observing the initial stages of formation of independent populations.

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