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HUMAN GENETICS

Dynamics of the Population Structure of Belgorod Oblast. Malecot's Isolation by Distance

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Abstract—The article presents the results of assessing the dynamics of parameters of Malecot's isolation by distance model among the population of Belgorod oblast from 1978–1980 to 2016–2018. When compared with data for 1890–1910 and 1951–1953 on average for the region, an increase in the root-mean-square distances between the places of birth of spouses was established taking into account long-distance migrations (6.9 times) and without them (13.3 times), as well as effective migration pressure (1.5 times), and there was a decrease in the coefficient of linear systematic pressure (11 times) and the effective population size (1.3 times). The level of local inbreeding decreased significantly among the urban population and remained unchanged among the rural population. The most pronounced changes in the parameters of Malecot's isolation by distance model occurred in the middle to the second half of the 20th century. The differences in most indicators of Malecot's isolation by distance model between city and village, maximally expressed at the end of the 19th century, decreased over the course of generations and were practically leveled out by 2016–2018.

Keywords: Malecot's isolation by distance model, local inbreeding

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INTRODUCTION

The study of population genetic characteristics of various population groups is carried out using various models, one of which is Malecot's isolation by distance model [1–3]. This model takes into account the influence of geographic distances on the genetic diversity of populations and allows us to assess the level of genetic differentiation of the population and determine factors that influence the genetic characteristics of the population [3]. Malecot's isolation by distance model has been successfully used since the end of the 20th century in many population studies of various ethnoterritorial population groups [3–15].

This communication continues the series of works [16, 17] devoted to the study of the dynamics of a number of population-demographic indicators among the population of the south of Central Russia and is a continuation of the study of the dynamics of the parameters of Malecot's isolation by distance model [17] among population of Belgorod oblast for period from 1951 to 2018.

MATERIALS AND METHODS

The object of this study is the inhabitants of district populations of Belgorod oblast: Belgorodsky, Starooskolsky, Novooskolsky, Korochansky, Grayvoronsky, Valuysky, Alekseevsky, Krasnogvardeisky. Detailed characteristics of the studied areas and criteria for their inclusion are presented in previously presented works [16, 17]. The study was conducted over three time periods: 1978–1980, 1991–1993, and 2016–2018.

The material was data from acts of civil status of the regional registry office archive for 1978–1980 (10991 records), 1991–1993 (4508 records), and 2016–2018 (5467 records), with a total volume of 20966 distances between the birthplaces of spouses. The methodological features of calculating the parameters of Malecot's isolation by distance are presented in previous works [14, 17]. The analysis was carried out at the district level [18]. To assess trends in dynamics of indicators of Malecot's isolation by distance model, data were used across five time periods: 1890–1910, 1951–1953, 1978–1980, 1991–1993, and 2016–2018 (the first two periods were discussed earlier [17]). Thus, we examined the dynamics of isolation parameters over a 130-year period (from 1890 to 2018).

In order to assess the relationship between the parameters of Malecot's isolation by distance and other studied population-demographic indicators (the proportion of marriages concluded between people from different regions, from the same region, from the same district, from the same village (these indicators

Table 1. Parameters of Malecot's isolation by distance model among the population of Belgorod oblast in 1978–1980

District	N	σ	σ'	m	k	M_e	N_e	a	b
Belgorodsky	3385	294.30	256.24	0.013	0.371	0.098	99219	0.00003	0.00173
city	2342	296.68	257.40	0.013	0.387	0.101	79372	0.00003	0.00175
village	1043	288.90	257.54	0.011	0.335	0.085	19847	0.00015	0.00160
Starooskolsky	2236	310.77	274.42	0.013	0.301	0.087	54186	0.00005	0.00152
city	1266	351.28	350.16	0.000	0.355	0.017	38677	0.00039	0.00052
village	970	248.12	171.40	0.023	0.242	0.107	15509	0.00015	0.00270
Novooskolsky	872	254.31	189.65	0.020	0.272	0.106	16480	0.00014	0.00243
Korochansky	863	210.38	137.74	0.023	0.301	0.119	15050	0.00014	0.00354
Grayvoronsky	497	274.14	224.01	0.015	0.274	0.092	10156	0.00027	0.00192
Valuysky	1249	242.16	180.81	0.019	0.285	0.106	74985	0.00009	0.00255
Krasnogvardeisky	1042	142.46	58.30	0.019	0.195	0.089	18268	0.00015	0.00722
Alekseevsky	847	218.82	138.62	0.023	0.292	0.118	29234	0.00007	0.00351
Average for the oblast	**1374**	**243.42**	**182.48**	**0.018**	**0.286**	**0.102**	**39697**	**0.00012**	**0.00305**
city	**1804**	**323.98**	**303.78**	**0.007**	**0.371**	**0.059**	**59025**	**0.00021**	**0.00114**
village	**1007**	**268.51**	**214.47**	**0.017**	**0.288**	**0.096**	**17678**	**0.00015**	**0.00215**

For Tables 1–3: σ—root-mean-square distance between the places of birth of spouses taking into account long-distance migrations; σ'—root-mean-square distance between the places of birth of spouses without taking into account long-distance migrations; m—half the share of long-distance migrations; k—half the share of intermediate migrations; M_e—effective migration pressure; N_e—effective population size; a—local inbreeding; b—coefficient of linear systematic pressure.

were presented earlier [16]), a correlation analysis was carried out (Spearman's rank correlation coefficient was calculated) for five time periods (the first two periods were considered previously [17]).

RESULTS

Parameters of Malecot's Isolation by Distance Model among the Population of South Central Russia

1. *1978–1980.* In 1978–1980, significant variability was revealed in most indicators of Malecot's isolation by distance model across districts of Belgorod oblast (Table 1). Maximum variability was found for the effective population size (9.8 times, from 10156 to 99219), local inbreeding (9 times, from 0.00003 to 0.00027), linear systematic pressure coefficient (4.8 times, from 0.000152 to 0.00722), and root-mean-square distances between birthplaces of spouses without accounting for long-distance migrations (4.7 times, from 58.3 to 274.42 km). The average local inbreeding value for the region was 0.00012. The minimum values of this indicator are typical of districts with the maximum effective population size, which include a large city—Belgorodsky (0.00003), Starooskolsky (0.00005), Alekseevsky (0.00007), Valuysky (0.00009). The maximum values of local inbreeding were observed in the Grayvoronsky district (0.00027), which experienced low migration pressure (0.092) with a minimum effective population size (N_e = 10156).

Analysis of the urban and rural population of Belgorod oblast showed that, in the city, on average, the effective population size is higher (by 3.3 times), and the root-mean-square distances between the places of birth of spouses are higher, taking into account long-distance migrations (by 1.2 times) and without them (by 1.4 times). The low value of local inbreeding (0.00021) is due to the fact that the effective population size in the city is on average 3.34 times higher, and the coefficient of linear systematic pressure and effective migration pressure are lower (1.9 and 1.6 times, respectively) than in rural areas (Table 1).

2. *1991–1993.* In 1991–1993, significant variability was established in terms of local inbreeding (16 times, from 0.00002 to 0.00029) and effective population size (14.4 times, from 8851 to 127708) (Table 2). Somewhat less variability was noted for the coefficient of linear systematic pressure (1.8 times, from 0.00191 to 0.00352), root-mean-square distances between the places of birth of spouses excluding long-distance migrations (1.7 times, from 135.44 to 230.34 km), and half the share of long-distance migrations (1.6 times, from 0.017 to 0.027).

The local inbreeding coefficient values were minimal (0.00002–0.00003) in areas with the maximum effective population size, which included a large city—Belgorod and Stary Oskol districts. The maximum

Table 2. Parameters of Malecot's isolation by distance model among the population of Belgorod oblast in 1991–1993

District	N	σ	σ'	m	k	M_e	N_e	a	b
Belgorodsky	1185	263.79	200.00	0.019	0.310	0.111	127708	0.00002	0.00236
city	957	256.18	189.80	0.019	0.312	0.116	103831	0.00002	0.00249
village	228	293.59	248.76	0.015	0.320	0.100	23877	0.00010	0.00180
Starooskolsky	677	272.05	218.87	0.017	0.305	0.103	72361	0.00003	0.00208
city	380	302.70	268.41	0.012	0.379	0.095	61333	0.00004	0.00163
village	297	226.87	153.71	0.020	0.222	0.097	11027	0.00023	0.00286
Novooskolsky	312	239.98	149.16	0.027	0.267	0.124	15605	0.00013	0.00334
Korochansky	362	287.83	204.43	0.025	0.262	0.117	13266	0.00016	0.00237
Grayvoronsky	235	293.99	230.34	0.019	0.236	0.097	8851	0.00029	0.00191
Valuysky	675	258.13	187.66	0.021	0.267	0.109	23958	0.00010	0.00249
Krasnogvardeisky	489	217.88	135.44	0.024	0.262	0.113	15561	0.00014	0.00352
Alekseevsky	573	259.73	179.48	0.023	0.246	0.108	21809	0.00011	0.00259
Average for the oblast	**564**	**261.67**	**188.17**	**0.022**	**0.269**	**0.110**	**37390**	**0.00012**	**0.00258**
city	**669**	**279.44**	**229.10**	**0.016**	**0.346**	**0.104**	**82582**	**0.00003**	**0.00206**
village	**263**	**260.23**	**201.23**	**0.018**	**0.271**	**0.099**	**17452**	**0.00017**	**0.00233**

Table 3. Parameters of Malecot's isolation by distance model among the population of Belgorod oblast in 2016–2018

District	N	σ	σ'	m	k	M_e	N_e	a	b
Belgorodsky	1128	262.31	210.31	0.017	0.301	0.103	170230	0.00001	0.00216
city	568	260.20	211.13	0.017	0.298	0.101	130518	0.00002	0.00213
village	560	264.43	209.53	0.019	0.303	0.105	39712	0.00006	0.00219
Starooskolsky	1187	252.65	185.86	0.019	0.228	0.096	86841	0.00003	0.00236
Novooskolsky	413	311.00	211.01	0.023	0.276	0.115	13733	0.00016	0.00227
Korochansky	360	273.81	207.99	0.019	0.281	0.106	13193	0.00018	0.00222
Grayvoronsky	333	266.07	195.41	0.021	0.251	0.105	9905	0.00024	0.00234
Valuysky	812	272.31	193.00	0.023	0.323	0.125	22029	0.00009	0.00259
Krasnogvardeisky	514	207.55	131.82	0.021	0.321	0.119	12250	0.00017	0.00370
Alekseevsky	720	209.58	115.64	0.024	0.303	0.122	20457	0.00010	0.00427
Average for the oblast	**683**	**256.91**	**181.38**	**0.021**	**0.285**	**0.111**	**43580**	**0.00012**	**0.00274**

values of local inbreeding (0.00029) were observed in the Grayvoronsky district, which experienced the lowest migration pressure (0.097) with a minimum effective population size (8851) (Table 2).

In urban populations, on average, the effective population size was 4.7 times higher, and the level of local inbreeding was 5 times lower compared to the rural population (Table 2).

3. *2016–2018.* In 2016–2018, the maximum variability was established for the effective population size (17.2 times, from 9905 to 170230) and local inbreeding (17.2 times, from 0.00001 to 0.00024) (Table 3). Somewhat less variability was noted for the coefficient of linear systematic pressure (2 times, from 0.00216 to 0.00427) and root-mean-square distances between the places of birth of spouses taking into account long-distance migrations (1.5 times, from 207.55 to 311.00 km) and without them (1.8 times, from 115.64 up to 211.01 km).

The minimum values of local inbreeding were observed in districts (Belgorodsky (0.00001) and Starooskolsky (0.00003)) characterized by a high level of urbanization and characterized by a maximum effective population size. The maximum value of this indi-

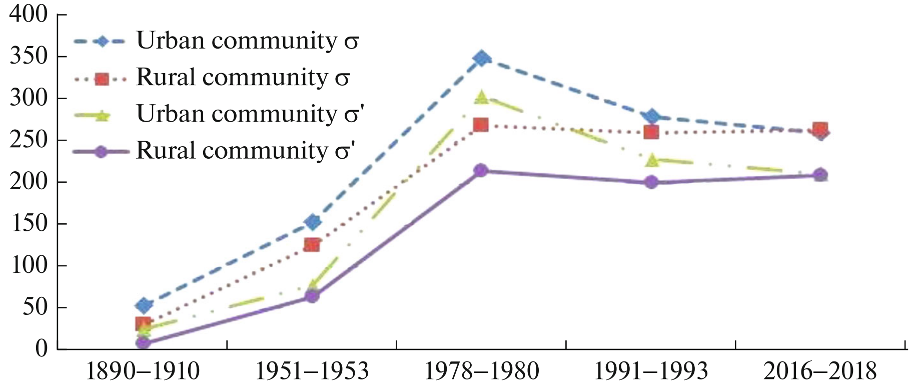

Fig. 1. Dynamics of root-mean-square distances between the places of birth of spouses taking into account long-distance migrations (σ) and excluding long-distance migrations (σ') among the urban and the rural population.

cator (0.00024) was found in the Grayvoronsky district, which experienced low migration pressure (0.0105) with a minimum effective population size (9905) (Table 3).

An analysis of the parameters of Malecot's isolation by distance model carried out for residents of Belgorod and the rural population of the Belgorod district showed that, despite approximately the same migration load, the value of local inbreeding in the city (0.00002) is 3 times lower, and the effective population size (N_e = 130518) is 3.3 times higher than among village residents. No significant differences were found in the other indicators of Malecot's isolation by distance model (Table 3).

Trends in the Dynamics of the Main Indicators of Malecot's Isolation by Distance Model among the Population of the South of Central Russia

At the final stage of the work, an analysis of the directions of the dynamics of the main indicators of Malecot's isolation by distance model from 1890–1910 to 2016–2018 was carried out in the context of five time periods (the first two periods were studied by us earlier [17]). The following multidirectional trends were identified.

Firstly, in the region, on average, the root-mean-square distances between the places of birth of spouses increased significantly taking into account long-distance migrations (by 6.9 times, from 37.40 to 256.91 km) and without them (by 13.3 times, from 13.62 to 181.38 km) with maximum dynamics from 1890–1910 to 1978–1980. Over the 130-year period, there was a decrease in the coefficient of linear systematic pressure (11 times) and an increase in the share of long-distance migrations (1.6 times), intermediate migrations (1.4 times), and effective migration pressure (1.5 times). The effective population size decreased over 130 years (1.3 times) with the sharpest decline in this indicator (3.6 times) from the end of the 19th century to 1951–1953 and gradual growth in subsequent generations. At the same time, over the studied 130-year period, the values of local inbreeding increased by 2 times and the dynamics of this indicator were diametrically opposed to changes in the coefficient of linear systematic pressure.

It should be noted that significant changes in the parameters of Malecot's isolation by distance model occurred in the mid-20th century (1951–1953) and the subsequent generation, as evidenced by sharp changes on the graphs—an increase in some indicators and a decrease in others.

Secondly, over the 130-year period, among the urban and rural population of the south of Central Russia, for most indicators of Malecot's isolation by distance, unidirectional trends in variability were noted (Figs. 1–5): an increase in the root-mean-square distances between the places of birth of spouses taking into account long-distance migrations and without them (Fig. 1) and effective migration pressure (Fig. 3), and a decrease in the coefficient of linear systematic pressure (Fig. 2). At the same time, among the rural population, more pronounced dynamics were observed in the root-mean-square distances between the places of birth of spouses taking into account long-distance migrations (9.6 times) and without them (22 times) (Fig. 1) and the coefficient of linear systematic pressure (19.3 times) (Fig. 2) compared to the urban population (4.9, 8.4, and 10 times, respectively).

The dynamics of the effective population size indicator among the urban and rural populations were in different directions (Fig. 4). In the urban part of the population, over 130 years, the values of the effective population size increased by 33.6 times, and in the rural part, they decreased by 1.3 times (Fig. 4).

The level of local inbreeding was characterized by reverse dynamics. So, if in 1890–1910 the value of local inbreeding in the city was 19.5 times higher than in the village, then by 2016–2018 the rate of local inbreeding became 3 times higher in the village compared to the city. At the same time, for the urban part

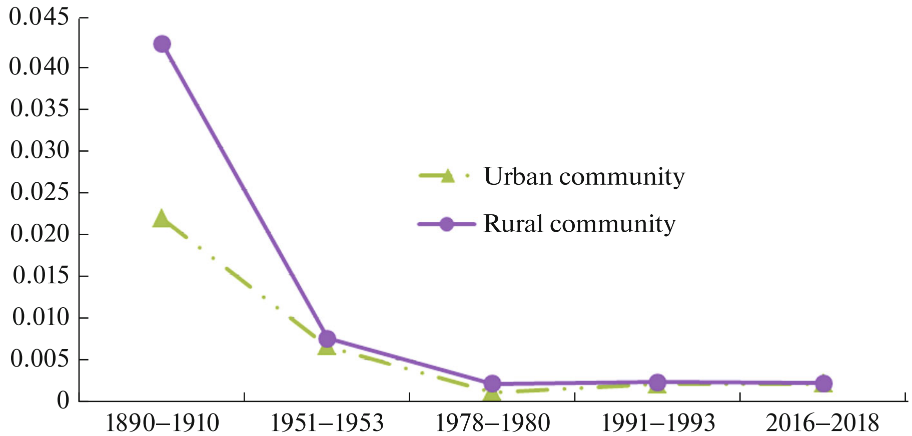

Fig. 2. Dynamics of linear systematic pressure coefficient (b) among the urban and the rural population.

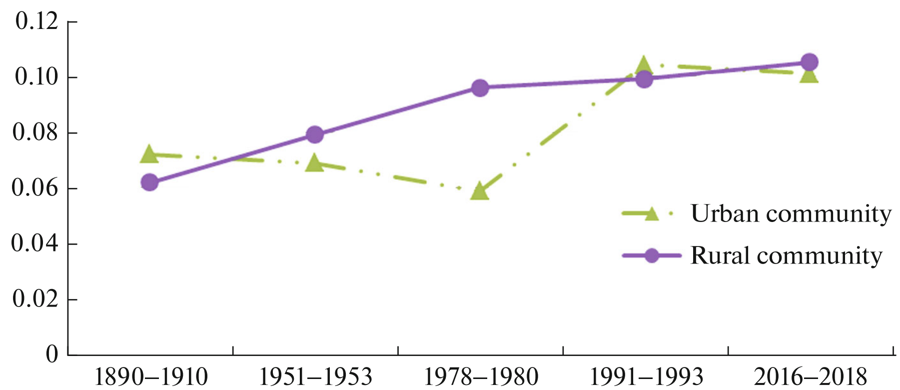

Fig. 3. Dynamics of effective migration pressure (M_e) among the urban and the rural population.

of the population, there was a consistently pronounced decrease in this indicator (78 times) throughout the entire period, while in the rural part there was variability over five periods with a decrease of only 1.3 times over 130 years (Fig. 5).

It is important to emphasize that, over the 130-year period, the differences in the vast majority of indicators of Malecot's isolation by distance model between city and village, maximally expressed at the end of the 19th century, decreased over a number of generations and were

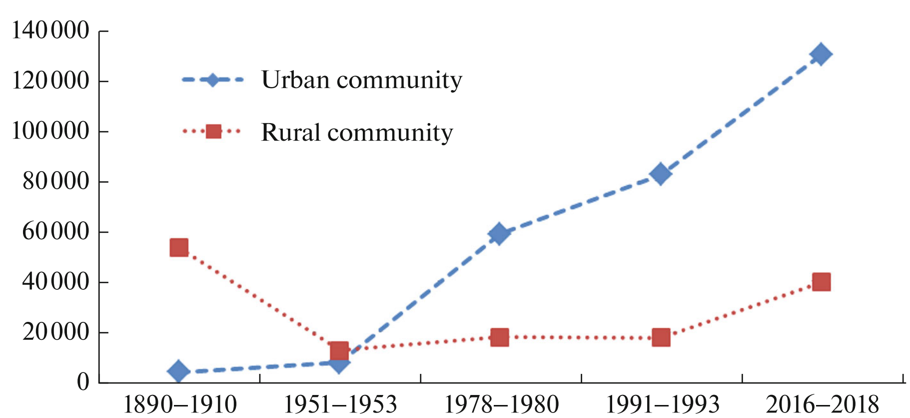

Fig. 4. Dynamics of effective population size (N_e) among the urban and the rural population.

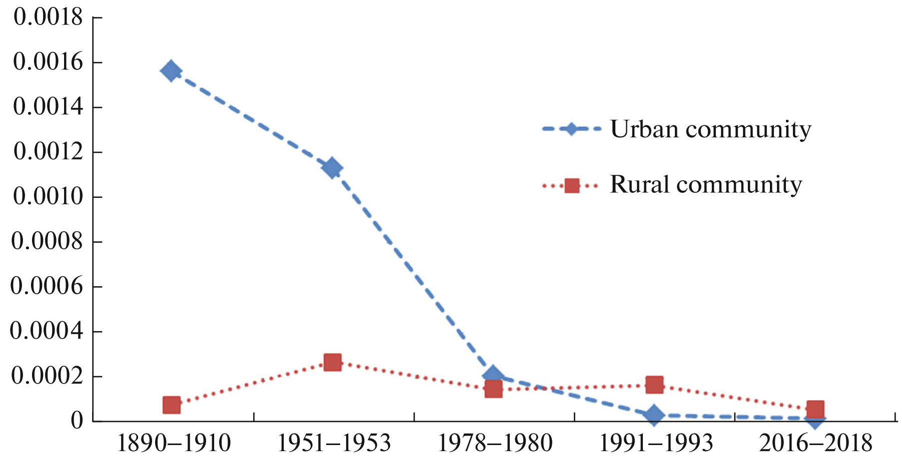

Fig. 5. Dynamics of local inbreeding (*a*) among the urban and the rural population.

practically leveled out by 2016–2018 (excluding effective population size and local inbreeding) (Figs. 1–5).

Thirdly, an analysis of the correlation relationships between the parameters of Malecot's isolation by distance and the marriage and migration characteristics of the population (previously presented in [16]) for five time periods (the first two periods were considered earlier [17]) (Table 4) showed that, with an increase in the proportion of marriages concluded between people from different regions and a decrease in the proportion of marriages concluded within the oblast and district, the root-mean-square distances between the places of birth of spouses increased taking into account long-distance migrations, and the coefficient of linear systematic pressure decreased. This trend and direction of correlation relationships were visible among the urban population and were absent among the rural population.

DISCUSSION

Analysis of the parameters of Malecot's isolation by distance model showed changes in the level of local inbreeding in the Belgorod population (more pronounced among the urban population). At the same time, over the 130-year period, the effective population size in Belgorod oblast decreased (1.3 times) with the sharpest decrease in this indicator (2.9 times) from the end of the 19th century to 1951–1953 [17] and its gradual growth in subsequent generations until 1991–1993. The reasons for these changes were described by us in the previous communication [17] and are associated with the administrative and territorial transformations of uezds into districts, the boundaries of which significantly decreased from the end of the 19th century to the beginning of the 21st century.

Belgorod oblast was formed within its modern borders in the postwar period—in 1954. The size of the region and the effective population size began to gradually increase, as we described in detail earlier [16]. The increase in migration inflow is evidenced by the growth of such indicators as the root-mean-square distances between the places of birth of spouses taking into account long-distance migrations (by 6.9 times, from 37.40 to 256.91 km) and without them (by 13.3 times, from 13.62 to 181.38 km), with maximum dynamics between 1890–1910 to 1978–1980. This indicates a significant expansion of the range of marriage migrations.

Over the period of time we studied, there was an increase in the effective pressure of migration (1.5 times) and the share of long-distance migrations (1.6 times) (this happened most significantly from 1951–1953 to 1978–1980). A pronounced decrease (11 times) in the linear systematic pressure coefficient was also recorded (with maximum dynamics from 1890–1910 to 1978–1980). Moreover, over the last two

Table 4. Significant Spearman correlation coefficients between the parameters of the model of isolation by distance and marriage migration in Belgorod oblast for five periods

Indicators studied	Proportion of people from different oblasts	Proportion of people from one oblast	Proportion of people from one district
Root-mean-square distances between the birthplaces of spouses (σ)	0.90 ($p = 0.037$)	–0.90 ($p = 0.037$)	–0.90 ($p = 0.037$)
Linear systematic pressure coefficient (b)	–0.90 ($p = 0.037$)	0.90 ($p = 0.037$)	0.90 ($p = 0.037$)

generations (from 1978–1980 to 2016–2018), the above indicators changed slightly.

Previously, L.A. Atramentova and O.V. Filiptsova, when studying the spatial characteristics of marriage migrations in the Belgorod population for 1960, 1985, and 1995, found an increase in marriage distances from 590 km to 891 km and a decrease in the indicator *b* from 0.00110 to 0.00062 over the study period, which indicated an "increase in the genetic efficiency of migration" [19].

It should be noted that the direction of the dynamics of most indicators of the parameters of the Malecot model for Belgorod oblast for 130 years demonstrates a trend similar to the Moscow population observed in approximately the same time interval (1892–1918, 1955, 1980, 1994–1995), with the exception of the scale of changes [9, 13, 20–22]. Thus, the degree of isolation by distance in Moscow in the mid-20th century compared to its beginning decreased by half, and by the end of the century, it decreased by two-thirds, while the variability in the value of effective migration pressure was minimal for 100 years, and in 1994–1995, it decreased. It should be noted that, in the Belgorod population, there was also minimal dynamics of the effective migration pressure indicator, but in contrast to the Moscow population, the effective migration pressure increased over 130 years (on average 1.3 times). The shares of "short" migrations and "long-distance" migrations increased in both the Moscow [11, 13] and the Belgorod population (our data).

A similar trend in the parameters of Malecot's isolation by distance model as in Moscow was observed in Donetsk (1960, 1985, 1992) [23], Kharkiv (1960, 1985, 1993) [24], and Poltava (1960, 1985, 1995) [25], where over more than 30 years, "long-distance" and "short-range" migrations increased and the degree of isolation by distance and the magnitude of effective migration pressure decreased [13, 23–25].

It should be noted that the dynamics of the main parameters of Malecot's isolation by distance differed among the urban and rural population of the Belgorod region. So, from the end of the 19th century to the beginning of the 21st century, the effective population size among the urban population increased (Fig. 4) and the level of local inbreeding decreased compared to the rural population (Fig. 5). Steady growth in the effective size of cities was observed from 1951–1953 and the next three generations until 2016–2018 (owing to the emergence of new young cities in the region). The effective size of the rural population remained virtually unchanged over this time period and increased only slightly over the past generation. Here, over a 130-year period, differences in most indicators of Malecot's isolation model by distance between city and village, maximally expressed at the end of the 19th century, decreased over a number of generations and were practically leveled out by 2016–2018 (excluding effective population size and local inbreeding).

The results of the dynamics of the indicators of Malecot's model of isolation by distance in the Belgorod region that we obtained are consistent with the data for the neighboring Kursk oblast [10, 26], where the dynamics of the Malecot indicators were previously analyzed for a 30-year period (1960–1963, 1987–1990). The coefficient of local inbreeding in the districts of Kursk oblast varied from 0.00005 in the Zheleznogorsk district to 0.00043 in the Ponyrovsky district, while in the neighboring Belgorod oblast (our data), it averaged 0.00012 (in 1991–1993). As in the Belgorod region, the districts of Kursk oblast, which included cities, were characterized by a minimal level of inbreeding (a = 0.00005–0.000087). However, in the cities of Belgorod oblast (our data), it was even lower (on average 0.00003 in 1991–1993). In most populations of Kursk oblast, a decrease in the coefficient of linear systematic pressure was found over the 30-year period, which is consistent with our data for the Belgorod region. The dynamics of local inbreeding in the Kursk region (as well as in the Belgorod region) were mainly determined by changes in the effective population size. Over the 30-year period, there was an increase in the effective population in cities (Kursk and Lgov) and in general in the Zheleznogorsk and Kurchatov districts (owing to the emergence of young cities) and its decrease in rural populations. For the period from 1960–1963 to 1987–1990, an increase in the average distance between the places of birth of spouses was found among the rural population and a decrease in these indicators among urban residents. The study noted that, over the last generation, differences in the radius of marriage migration between the urban and rural populations of the region decreased. In contrast to Belgorod oblast, the level of local relatedness and the coefficient of linear systematic pressure in all populations considered among the rural and urban population, except for the Zheleznogorsk district, were the same [10, 26].

It should be noted that the values of local inbreeding among the population of the Belgorod oblast do not stand out from the range of those values for other Russian populations but differ significantly from similar indicators of isolated and "native" populations [11–13, 27]. For example, our data are consistent with the results of previously conducted studies among the Russian population of Kostroma oblast (in Sharinsky district, a = 0.000161; in Buysky district, a = 0.000161) [28], Kirov oblast (a = 0.000106–0.001495) [29, 30], and Arkhangelsk oblast (in Vinogradsky district, a = 0.000565; in Krasnoborsky district, a = 0.000472) [31], but lower than in Tver oblast (in Ostashkovsky district, a = 0.00110; in Udomelsky district, a = 0.0045) [32] and in Semipalatinsk oblast (Abaisky district, a = 0.0003) [33]. Russian rural populations corresponded to local inbreeding of Udmurts, which varied from 0.00027 in the Igrinsky district to 0.00065 in Debessky district (on average a = 0.00035) [34, 35] and Circassians (a = 0.00034) (average value for

Karachais at the end of the 20th century $a = 0.00029$) [36].

Local inbreeding values somewhat different from the above-mentioned Russian populations have been established for the peoples of the Caucasus and the Volga region: Adyghe Autonomous Oblast of Krasnodar krai ($a = 0.00397$) [11], Republic of Chuvashia (in the city, $a = 0.000189$; in the district, $a = 0.000318$) [12], Republic of North Ossetia-Alania (Kumyks of Mozdoksky district, $a = 0.00067$) [36, 37], and Karachay-Cherkess Republic ($a = 0.00007–0.00304$; 0.0017–0.0047 for Circassian villages and from 0.001 to 0.003 for Abaza villages) [27, 38–40], as well as for Tatarstan ($a = 0.0001–0.0008$; for Tatars, $a = 0.00170–0.00291$) [41] and Bashkortostan (for Bashkirs of six rural districts, $a = 0.00012–0.00074$) [42].

It should be noted that numerous studies have shown the important medical and genetic significance of the parameters of population isolation (local inbreeding, migration, etc.), which affect the prevalence of both monogenic hereditary pathology and other hereditary diseases among the population [22, 27–29, 31–33, 35, 43]. In this regard, these indicators must be taken into account when planning population genetic and medical genetic studies [44–51].

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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