EVOLUTIONARY STUDIES ON THE DISTRIBUTION AND DYNAMICS OF MELANISM IN THE HAMSTER (CRICETUS CRICETUS L.). I. DISTRIBUTION OF BLACK HAMSTERS IN THE UKRAINIAN AND BASHKIRIAN SOVIET SOCIALIST REPUBLICS (U.S.S.R.)[1]

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THE PROBLEM of natural selection is one of the most important and, at the same time, least investigated in evolutionary biology. It has been treated chiefly through rather elaborate mathematical calculations based on *a priori* assumptions, since actual observations have been scarce and the data obtained meagre. The most promising method for investigating the laws of natural selection is detailed study of changes which take place in wild populations of a species in the course of several generations. Of course, changes in the frequencies of different types of individuals in a population may depend not only on natural selection but on other factors as well, such as chance survival, migration, etc. Where the biology of the organisms concerned is insufficiently known, it may be difficult to evaluate the part played by natural selection in the complex of factors which influence the structure and composition of the populations. On the other hand, there remains the possibility of tracing the actual mechanisms of the transformation of wild populations by natural selection and of discovering the paths by which new races and varieties are created.

The common hamster (*Cricetus cricetus* L.) provides favorable material for studies of this kind. Its natural populations often contain considerable proportions of melanic individuals—that is, they are dimorphic with respect to an easily classifiable trait. Such differences in coat color in rodents are hereditary and are highly independent in their expression from environmental modification. As shown by GERSHENSON and POLEVOI (1940, 1941) and GERSHENSON (1941), the black coat color in the hamster is inherited as a simple autosomal dominant, and the matings between black and normal hamsters occur in wild populations at random. Different populations contain diverse proportions of melanic individuals. As with most rodents, the hamster breeds rapidly, and its biology is well known. These rodents are the object of a fairly developed branch of fur trade. Data concerning the proportions of black and normal hamsters trapped during a number of years by several factories of "Soiuspushnina" (All-Union Fur Syndicate) located in two different geographical zones of the European part of U.S.S.R., in the Ukraine and in Bashkiria were made available for the study reported here. This provided far more material

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than could be obtained through field collections alone. Since in the hamster the generations overlap, and since the duration of the reproductive period is not exactly known, the calculations necessary to determine the intensity of natural selection are necessarily complicated.

Extraction of the pertinent data from the archives of "Soiuspushnina" was a laborious process which required careful examination of many thousands of records of local factories. The author wishes to acknowledge obligation in the fulfillment of this task to I. GRUSHEVSKAIA, M. ILCHENKO, and I. LITOSHENKO.

LITERATURE REVIEW

The existence of black hamsters has been known for a long time. As early as 1769, PALLAS (1771) observed considerable numbers of them near Simbirsk (now Ulianovsk), and later (PALLAS 1778) he reported their presence in other localities of the Volga region, especially near Kazan, and in the Ural region, especially near Ufa. LEPEKHIN (1771) likewise found black hamsters near Simbirsk and in the former Ufa province during his journey in 1768–69. GEORGI (1775) pointed out that in 1772 black hamsters were frequent near Kazan where their pelts were extensively used in the fur industry. About the same time SULZER (1774) and BECHSTEIN (1789, 1807) found them in the western part of the species area in Thuringia, Germany.

In the nineteenth century, LÜBEN (1848) mentioned the existence of black hamsters in Saxony, EVERSMANN (1850) along the rivers Belaia, Kama, Volga, and throughout the Kazan province, where they are more frequent than normal ones, and KESSLER (1851) near Zolotonosha (in the vicinity of Poltava). According to BOGDANOV (1871), only black hamsters are to be found in the northern part of the former Kazan province, while in the southwestern part, as well as in the former Saratov and Simbirsk provinces, exclusively normally colored hamsters occur. KARELIN (1875) recorded black hamsters in the Ural region.

Much information about black hamsters has appeared since the beginning of the present century. According to KRULIKOVSKY (1902), exclusively black hamsters are found in the former Viatka province, but according to SCHITKOFF (1905), they are rather rare in the former Simbirsk province but very frequent near Kazan, where they completely supplant in some places the normal ones. SIMROTH (1905, 1906) presented data on black hamsters in Thuringia, BYKOVSKY (1913) and STACH (1920) in the neighborhood of Tarnopol, KRYZHOV (1935) near Dniepropetrovsk, and JAKOBI (1928) re-examined the black hamster situation in Thuringia. KRYSHTAL (1929) gave detailed information about black hamsters collected near Berdichev; PIDOPLICHKA (1928, 1930a) reported their occurrence in the part of the Ukraine west of the Dnieper, ARGIROPULO (1931) near Kurgan, NOVIKOV (1932) found them in the Caucasus and near Gomel, KUZNETSOV (1932) in Tataria and Bashkiria, KUNTZE and SZYNAL (1933) in different localities of the western Ukraine, and KIRIKOV (1934) in different districts of Bashkiria and near Gorky and Rostov-on-Don. DIAKONOV and SULLA (1935) also reported on frequency of black hamsters in Bashkiria.

PETZSCH (1936) in a monograph on the biology of reproduction of the hamster included detailed data on the distribution of the black coat color in Germany. MIGULIN (1938) in a review of Ukrainian mammals stated that black hamsters exist near Kharkov and that apparently their distribution in the Ukraine is much wider than is indicated in the literature. Papers by TIMOFEEFF-RESSOVSKY (1939a, 1939b) attempt to give a picture of the distribution and dynamics of black hamsters during the last 150 years.

Some authors have attempted to define the ecological conditions under which black hamsters are especially frequent. Thus, it was SCHITKOFF's (1905) opinion that they are found predominantly on clay soil covered with oak or mixed forests. SIMROTH (1906) connected their appearance in Thuringia with an exceptionally hot summer. HILZHEIMER (1913) suggested that in the Volga region they are most frequent in moist places, and KIRIKOV (1934) regarded them as chiefly a forest and river bank form. According to PETZSCH (1936), black hamsters increase in frequency in years when the total numbers of hamsters are great and decrease in years when hamsters are scarce. TIMOFEEFF-RESSOVSKY (1939a) observed that black hamsters are especially frequent in the cool and humid climate near the northern border of the distribution area of the species.

Descriptions of the melanic hamsters given by various authors coincide with one another fairly well. In all cases it is stated that melanic hamsters are totally black, with the exception of feet, tail, nose, upper lip, and margins of the ears, which are covered with white hair; in some cases white spots are present on the throat and chest. According to STACH (1920), black hamsters from the vicinity of Tarnopol have white margins of the ears and white feet; the rest of the body is black, but behind the ears and near the tail a reddish tinge is discernible. A detailed examination shows that each hair is not self-colored but gray at base, reddish in the middle, and black near the tip. This is especially clearly seen on the back and near the tail. Some individuals have white hairs on the upper lip; sometimes one or two longitudinal reddish stripes are present on the back. Besides these typical melanics, a much rarer type characterized by the presence of large irregular white spots has been reported (PALLAS (1789) and KIRILOV (1934) from the Ural region, BECHSTEIN (1789, 1807) in Thuringia). Such spotted black hamsters occur only in localities in which the usual melanics occur also. BOGDANOV (1871) and PETZSCH (1936) have observed that black hamsters are somewhat larger than normally colored ones, but other authors (for example, KESSLER 1851) have found no such size difference.

The taxonomic rank of black hamsters has been evaluated differently by different authors. PALLAS (1778) pointed out that they do not form a separate species, since they mate with normal ones and are often found together with the latter in the same litters. LEPEKHIN (1771) also ranked them as a variety but thought that they breed true. SCHREBER (1792) was first to regard black hamsters a subspecies, and TROUESSART (1910) gave them the name *Cricetus cricetus niger* Schreb. SIMROTH (1906) called them a mutation, STACH (1920) a "morpha," KIRIKOV (1934) defined them essentially as an ecotype.

The inheritance of the black coat color attracted the attention of several investigators. FISCHER (1874) attempted to solve this question experimentally, but his description of the crosses is so confused that no conclusions can be drawn. KRYSHTAL (1929) and PETSZCH (1936) examined ten or fewer litters of hamsters collected in nature and concluded that the black coloration is due to a recessive gene. Reinvestigation of this problem by GERSHENSON and POLEVOI (1940, 1941) on incomparably greater material definitely showed that melanism in the hamster is due to a simple autosomal dominant, probably homologous to the gene E^D for dominant black coloration known in the rabbit and in the black rat.

MATERIAL AND METHODS

The present work is based on the records of hamster pelts purchased by the local factories of "Soiuspushnina" in different districts of Ukraine in 1934–1939 (about two millions) and on field collections by the author made in 1939–1941. The data for Bashkiria come from records of 49 districts of "Soiuspushnina" and embrace more than one million hamsters trapped in the summer of 1933 and during the years 1937–1939.

In all, data of 529 district factories in the Ukraine covering about 445,000 square kilometers were available. The average territory covered by a factory is about 840 square kilometers, but the factories are not distributed evenly. Moreover, factories located in larger settlements, railway stations, and river ports may possibly obtain pelts from greater territories than factories in small and distant villages. The records of the district factories give the numbers of pelts purchased each month, the normal and the black pelts being recorded separately, since the latter are purchased at a higher price than the former. The district factories in Bashkiria cover a territory of about 140,000 square kilometers. The average territory covere dby a factory is here about 2,800 square kilometers, or more than three times larger than in the Ukraine, but the factories are distributed unevenly, being more numerous in the western and central than in the sparsely populated eastern part of the country.

It is important to examine the possible sources of errors in the records of "Soiuspushnina" factories with respect to the numbers of normal and black hamsters found in the different districts. Hamster pelts differ so clearly from those of other species of mammals, and the population is so well acquainted with hamsters, that misclassification of the species is very unlikely; examination of extensive material in the storehouses of "Soiuspushnina" revealed no instances of misclassification. Pelts of normal and of black hamsters are so sharply different from each other that mistakes in classification are excluded. Only in Bashkiria a slight error in classification is possible. As shown by KIRIKOV (1934), in some districts of Bashkiria, chiefly in the north, some of the black hamsters have white spots. At the fur factories most of these spotted blacks (those in which white hairs cover less than a quarter of the body surface) are classified as "Black," whereas a small minority in which the white spots are more extensive than one-quarter of the body are counted among the "Normals." As a result, the records of "Soiuspushnina" in Bashkiria may show

a slightly reduced frequency of the melanics. Hamsters are caught either by digging them out, by flooding their holes with water, or by setting traps at the entrance of the holes. No selection with respect to the coat color can occur. The hunting population does no use hamster pelts for its own needs and sells all the pelts to "Soiuspushnina."

As shown below, the frequency of black hamste s may vary greatly from district to district in the same region and also between localities within a district. Since trappers may be more active in some parts of a district than in others, the records of "Soiuspushnina" may not show the true frequencies of the black and normal hamsters within the district. This distortion, however, is not very serious; the number of trappers in each district is usually several dozen, and their hunting territories overlap each other so that the chance variations in the activities of the individual trappers are levelled off in the total. The records of the "Soiuspushnina" factories reflect, therefore, the actual

TABLE 1

Comparison of the frequencies of black hamsters observed during field work and those indicated by the records of "Soiuspushnina."

DISTRICT	TOTAL EXAMINED	NUMBER OF BLACK	PERCENTAGE BLACK
Malo-Devitsa, "Soiuspushnina"	6798	1781	26.2±0.5
Malo-Devitsa, Author's observations	694	172	24.8±1.6
Novo-Bassan, "Soiuspushnina"	585	23	3.9±0.8
Novo-Bassan, Author's observations	118	4	3.4±1.7

frequencies of the normal and black hamsters in the respective districts with a reasonable accuracy. This conclusion is confirmed by checking the records of "Soiuspushnina" in some districts against the results of observations made by the author during field work in the Malo-Devitsa district of the Chernigov region in July and August of 1939, and in the Novo-Bassan district of the same region in September of 1940 (table 1). The agreement between the data of "Soiuspushnina" and those of the author is very good.

DISTRIBUTION OF BLACK HAMSTERS IN THE UKRAINIAN S.S.R.

A summary of the data concerning the total number of hamsters and the number of black hamsters trapped in 1934–1939 in different regions of the Ukrainian S.S.R. is given in table 2. Data from 529 district factories, were available for the study, but the records of only 386 of those which had purchased more than 100 pelts during the respective years were used.

The frequencies of black hamsters differ not only in different regions of the Ukrainian S.S.R. but also in different districts within a region. Within a district, however, th: frequency of black hamsters is relatively constant from year to year. This can be seen by plotting the data for the different years on maps and comparing the maps. A more precise method is to determine the correla-

TABLE 2

Number of normal and black hamsters trapped in different regions of the Ukrainian S.S.R. during 1934–1939.

REGIONS	1934			1935			1936			1937			1938			1939			TOTAL		
	TOTAL	BLACK	PERCENTAGE OF BLACK	TOTAL	BLACK	PERCENTAGE OF BLACK	TOTAL	BLACK	PERCENTAGE OF BLACK	TOTAL	BLACK	PERCENTAGE OF BLACK	TOTAL	BLACK	PERCENTAGE OF BLACK	TOTAL	BLACK	PERCENTAGE OF BLACK	TOTAL	BLACK	PERCENTAGE OF BLACK
1. Vinnitsa	No data			38,508	16	0.04	44,250	502	1.13	2,506	31	0.12	33,436	646	1.93	14,331	488	3.41	155,586	1,683	1.08
2. Voroshilovgrad	3,114	1	0.03	1,114	0	0.00	764	1	0.13	1,508	1	0.06	1,320	0	0.00	No data			7,820	3	0.04
3. Dniepropetrovsk	32,551	45	0.14	12,480	62	0.50	26,521	29	0.11	30,127	19	0.63	16,769	93	0.55	No data			118,448	248	0.21
4. Zhitomir	No data			9,349	42	0.45	28,807	1,159	4.02	16,903	533	3.15	14,882	347	2.33	13,055	499	3.82	82,996	2,580	3.11
5. Zaporozhie	4,429	1	0.02	2,387	0	0.00	3,673	0	0.00	3,500	0	0.00	3,005	0	0.00	1,086	0	0.00	18,079	1	0.01
6. Kamenets-Podolsk	No data			17,229	249	1.45	99,614	4,239	4.26	90,883	4,069	4.48	67,608	3,948	5.84	57,668	3,635	6.30	333,002	16,140	4.85
7. Kiev	No data			45,912	329	0.72	23,307	288	1.24	28,367	475	1.67	45,290	930	2.05	45,251	1,158	2.56	188,127	3,180	1.69
8. Kirovograd	17,063	1	0.01	10,112	4	0.04	13,822	3	0.02	18,997	3	0.02	15,634	16	0.10	6,648	8	0.12	82,276	35	0.04
9. Nikolaev	No data			2,134	0	0.00	4,692	0	0.00	4,741	47	0.99	3,189	0	0.00	2,306	0	0.00	17,062	47	0.27
10. Odessa	No data			3,494	7	0.20	7,841	38	0.48	5,841	34	0.58	16,066	285	1.77	6,458	107	1.66	39,700	471	1.12
11. Poltava	21,277	2,326	10.93	20,603	3,158	15.33	30,446	2,616	8.59	48,262	3,218	6.67	47,260	2,438	5.16	No data			167,848	13,756	8.20
12. Stalino	13,932	765	5.49	5,182	173	3.33	9,787	55	0.56	8,235	218	2.65	4,685	0	0.00	No data			41,821	1,211	2.90
13. Sumy	3,726	39	1.05	20,110	25	0.12	16,170	113	0.70	26,304	247	0.87	29,061	74	0.25	No data			97,371	498	0.51
14. Kharkov	5,120	34	0.66	3,897	88	2.26	5,862	188	3.21	11,596	416	3.59	6,481	177	2.73	No data			32,956	903	2.74
15. Chernigov	No data			73,018	1,300	1.78	78,610	2,508	3.19	93,586	1,962	2.10	173,708	5,398	3.11	163,611	8,645	5.28	582,533	19,813	3.40
Grand total	101,212	3,212	3.17	265,529	5,453	2.05	394,166	11,739	2.80	415,911	11,273	2.71	478,393	14,353	3.00	310,414	14,540	4.68	1,965,625	60,570	3.08

tion coefficients between the frequencies of black hamsters within a district in different years. The correlation coefficient for successive years calculated from the data of 386 district factories is $+0.66 \pm 0.02$. The average frequencies of black hamsters during the entire period for which data are available are therefore satisfactory characteristics of the respective districts. A considera-

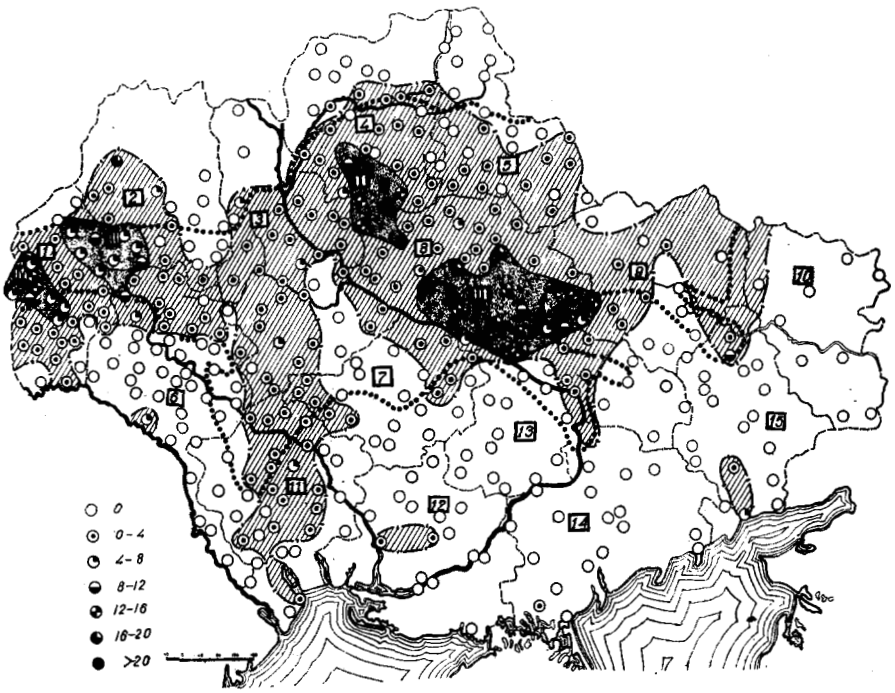

FIGURE 1. Distribution of black hamsters in the Ukrainian S.S.R. in 1934–1939. Stippled area—the distribution of melanics. I, II, III, IV—zones of high frequency of melanics. 1—Kamenets-Podolsk region; 2—Zhitomir region; 3—Kiev region; 4—Chernigov region; 5—Sumy region; 6—Vinnitsa region; 7—Kirovograd region; 8—Poltava region; 9—Kharkov region; 10—Voroshilovgrad region; 11—Odessa region; 12—Nikolaev region; 13—Dniepropetrovsk region; 14—Zaporozhie region; 15—Stalino region. Dotted line—boundaries of the forest-steppe zone. Circles—frequency of melanics in percentage. Scale in kilometers.

tion of changes in the frequencies from year to year is given in the following paper.

The map of the Ukraine in figure 1 shows the boundaries of the territory in which black hamsters were recorded in 1934–1939. The data of all factories, regardless of the numbers of hamster pelts they purchased, are included in this map provided any black hamsters were encountered among them. It may be seen from the map that the main distribution area in the Ukraine is practically continuous. Aside from this main area, there exist five "islands" where black hamsters are found surrounded by districts where no blacks were observed during the period studied. The "island" at the southwestern boundary may in reality be connected with the main area. BYKOVSKY (1913), STACH

(1920), and KUNTZE and SZYNAL (1933) found black hamsters near Tarnopol, Lvov, and north of Stanislav. This is confirmed by unpublished observations of RESHETNIK who did some field work in that region in 1940, and also by some preliminary data obtained by the writer in 1940 from the fur factories in that region (in some localities near Lvov and Tarnopol up to 10 per cent of black hamsters are found in the populations). The other four "islands," however, are independent of the main area. In each of two of them, that are located in the Chernigov region and near Odessa, a single black hamster was trapped among approximately 40,000 and 1,200 normals respectively. The "islands" in the Nikolaev and Stalino regions are doubtless real, though the frequency of melanics is very low in both of them.

Figure 1 indicates that within the main area of distribution there exist four zones in which the frequencies of the melanics are especially high. These zones

TABLE 3

Frequencies of black hamsters within a 20 kilometers broad strip of land lying inside and a similar strip lying outside the boundaries of the zones of high frequencies of melanics.

ZONE	INSIDE 20 KILOMETERS STRIP			OUTSIDE 20 KILOMETERS STRIP		
	NUMBER OF POINTS	AVERAGE PERCENTAGE	RANGE OF PERCENTAGES	NUMBER OF POINTS	AVERAGE PERCENTAGE	RANGE OF PERCENTAGES
I	8	17.58	10.67–27.14	11	1.49	0.00–4.52
II	11	16.07	5.00–41.48	13	1.68	0.00–3.80
III	7	8.87	6.34–13.52	9	3.45	0.51–4.40
IV	8	7.46	5.31–10.45	10	1.95	0.00–4.85

are marked in figure 1 by Roman numerals I to IV. In each of the four zones the frequency of black hamsters exceeds 5 per cent and may reach 20 per cent and higher. The first zone is located in the southern part of Chernigov and the adjacent part of Poltava regions. The second lies in the southeastern part of the Poltava region. The third is in the western part of the Kamenets-Podolsk region, and probably extends westward into the territory not considered in the study. The fourth lies in the northeastern part of Kamenets-Podolsk, northwestern part of Vinnitsa, and southwestern part of Zhitomir regions.

It is interesting to note that the outlines of these zones are nearly everywhere very sharp. This is shown in figures 2 and 3 which give exact average frequencies of black hamsters within, and in the immediate vicinity of, the Chernigov and Poltava zones of high frequency of black hamsters. Table 3 summarizes the frequencies of black hamster within a 20 kilometer broad strip of territory lying inside and one lying immediately outside the boundaries of each of these four zones.

The data presented in figures 2 and 3 and in table 3 show that the percentages of black individuals take a sharp drop at the boundaries of the zones outlined above, the transition being accomplished within a distance not exceeding

40 kilometers and in many places (for example, at the northeastern boundary of the first zone and the northern and southwestern boundaries of the second zone) within 10–15 kilometers. Examination of the parts of the territory from which data are available from points located close to each other suggests that such sharp transitions are characteristic of all four zones. Cases are not infrequent where a point lying within a zone constantly shows very high percentages of black hamsters, and another point lying just outside the zone as con-

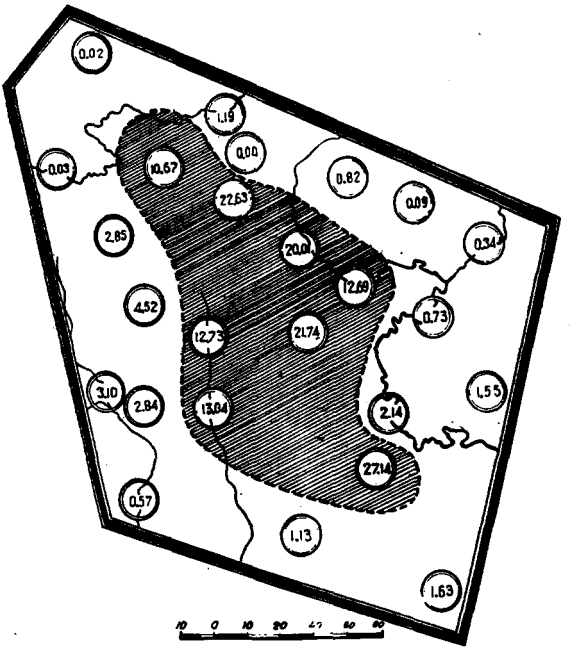

FIGURE 2. The Chernigov zone of high frequency of melanics. Circles—frequency of melanics in percentage. Scale in kilometers.

stantly shows very low percentages. The following examples may illustrate this. Losinovka and Talalaevka (first zone) are 12 kilometers apart and show 22.63 and zero per cent of melanics respectively; Grebenka (27.14 per cent) and Piriatin (2.14 per cent) in the first zone are 18 kilometers apart; Gradizhsk (22.05 per cent) and Novogeorgievsk (0.05 per cent) in the second zone are 15 kilometers apart; Felshtin (13.52 per cent) and Yarmolinzy (1.03 per cent) in the third zone are separated by only 9 kilometers.

Outside the four zones lie numerous districts with much lower frequencies of black hamsters. Such districts constitute a majority of all districts of the Ukraine in which melanics were recorded during the period investigated, and have usually one per cent of black hamsters or less. No classification of these districts on the basis of the frequencies of melanics in them can safely be made. Observation indicates that in the vicinity of the zones of high frequency of melanics (especially zones I and II) the percentage of black hamsters is some-

TABLE 4

Total number of hamsters and number of black hamsters trapped in 1933 and in 1937–1939 in different districts of the Bashkirian A.S.S.R.

DISTRICT	MAY–AUGUST 1933			1937			1938			1939			TOTAL FOR 1937–1939		
	TOTAL	BLACK	PER-CENTAGE OF BLACK	TOTAL	BLACK	PER-CENTAGE OF BLACK	TOTAL	BLACK	PER-CENTAGE OF BLACK	TOTAL	BLACK	PER-CENTAGE OF BLACK	TOTAL	BLACK	PER-CENTAGE OF BLACK
1. Abzelilovo	193	0	0.00	2,610	0	0.00	2,976	0	0.00	932	0	0.00	6,518	0	0.00
2. Arkhangelskoie	4,631	1,598	34.50	9,148	4,434	48.47	7,705	3,918	50.85	3,030	1,421	46.90	19,883	9,773	49.15
3. Askino		No data		12,804	7,512	58.67	21,286	11,726	55.09	13,514	7,447	55.11	47,604	26,685	56.02
4. Aurgazy	1,033	156	15.10	712	145	20.36		No data			No data		712	145	20.36
5. Baikibashevo		No data			No data			No data		1,977	1,407	71.17	1,977	1,407	71.17
6. Baimak	1,423	0	0.00	1,272	0	0.00	1,113	0	0.00	3.32	0	0.00	2,717	0	0.00
7. Bakaly	989	38	3.84	1,104	29	2.63		No data			No data		1,104	29	2.63
8. Baltachevo	503	306	60.83	13,250	9,159	69.12	46,241	32,848	71.04	19,432	13,578	69.87	78,923	55,585	70.43
9. Belebei	314	0	0.00	52	1	1.92		No data			No data		52	1	1.92
10. Belokatai	1,567	278	17.74	8,328	1,103	13.24	16,506	1,794	10.87	14,685	1,787	12.17	39,519	4,684	11.85
11. Beloretsk	335	5	1.49	441	12	2.72	1,054	30	2.84	477	5	1.05	1,972	47	2.38
12. Birsk	12,617	5,843	46.31	12,417	8,954	72.11	22,361	16,096	71.98	14,955	10,360	69.27	49,733	35,410	71.20
13. Blagoveshchensk	786	511	65.01	5,802	4,351	74.99	12,816	9,774	76.26	8,210	5,937	72.31	26,828	20,062	74.78
14. Buraevo	1,485	1,048	70.57	18,116	14,670	80.98	38,280	28,632	74.80	13,858	10,503	75.79	70,254	53,805	76.59
15. Burzian	51	0	0.00	221	1	0.45	1,319	0	0.00		No data		1,540	1	0.06
16. Buzdiak	4,577	477	9.77		No data			No data			No data			No data	
17. Chekmagushevo	5,385	939	17.44		No data			No data			No data			No data	
18. Chishmy	405	37	9.14		No data			No data			No data			No data	
19. Davlekanovo	674	42	6.23		No data			No data			No data			No data	
20. Diurtiulli	5,286	1,021	19.32	2,236	1,097	49.06		No data		258	151	58.53	2,494	1,248	50.04
21. Duvan	3,244	447	13.78	187	25	13.37	5,868	703	11.98	4,426	319	7.21	10,481	1,047	9.99
22. Iglino	520	453	87.12	7,533	5,498	72.99	7,164	5,021	70.09	2,663	1,920	72.10	17,360	12,439	71.65
23. Kaltasy	2,685	1,259	46.89	8,343	5,442	65.23	26,874	18,140	67.50	7,248	4,799	66.21	42,465	28,381	66.83
24. Karaidel	3,091	1,698	54.93	7,559	5,019	66.40	19,468	12,419	63.79	8,330	5,205	62.48	35,357	22,643	64.04
25. Karmaskaly	791	222	28.07		No data			No data			No data			No data	
26. Khaibullino	1,218	0	0.00	1,600	0	0.00	419	0	0.00	738	0	0.00	2,757	0	0.00
27. Kigi	151	1	0.66		No data			No data			No data			No data	
28. Krasnokamsk		No data		9,250	3,668	41.82	23,478	10,641	45.32	11,812	4,916	41.62	44,540	19,425	43.61
29. Krasnousolsk	2,188	285	13.02	18,725	1,989	10.62	31,910	4,620	14.48	8,230	1,249	15.18	58,865	7,858	13.35
30. Kugarchi	146	0	0.00	3,611	0	0.00	12,518	0	0.00	8,703	0	0.00	24,832	0	0.00
31. Kushnarenkovo	1,053	203	19.28	467	153	32.76	1,839	551	29.96	2,201	503	22.85	4,507	1,207	26.78
32. Makarovo	2,828	28	0.99	12,161	365	3.00	32,268	737	2.28	10,001	193	1.93	54,430	1,295	2.38
33. Maloyaz		No data		4,002	49	1.25	10,621	223	2.10	8,298	161	1.94	22,921	433	1.89
34. Mechetlino	1,138	148	13.01		No data			No data			No data			No data	
35. Meleuz	994	0	0.00	11,841	14	0.12	18,956	182	0.96		No data		30,797	196	0.64
36. Mishkino	209	177	84.69	15,675	12,070	77.00	50,381	38,446	76.32	26,661	21,179	79.44	92,717	71,695	77.34
37. Miyakino	2,190	21	0.96	2,640	49	1.86	8,556	18	0.21	2,872	20	0.70	14,068	87	0.62
38. Nurimanovo	4,070	2,771	68.08	14,949	12,133	81.16	23,274	19,118	82.14	12,907	10,523	81.53	51,130	41,774	81.70
39. Sterlitamak	4,765	195	4.09	1,901	151	7.94	3,312	221	6.67	615	42	6.83	5,828	414	7.10
40. Tatyshly		No data		8,109	5,876	72.46	16,393	12,244	74.74	7,620	5,414	71.05	32,112	23,534	73.29
41. Tuimazy	1,732	48	2.77	365	2	0.55	5,046	9	0.18	3,450	11	0.35	8,861	22	0.25
42. Uchaly	39	0	0.00		No data			No data			No data			No data	
43. Ufa	2,410	1,080	44.81	7,161	2,289	31.96	10,222	4,260	41.67	2,507	791	31.55	19,890	7,340	36.90
44. Uluteliak		No data			No data			No data		76	59	77.63	76	59	77.63
45. Voskressensk		No data			No data			No data		594	6	1.01	594	6	1.01
46. Yanaul	6,309	4,574	72.50	19,137	13,836	72.30	29,283	21,996	75.12	11,167	7,859	70.38	59,587	43,691	73.32
47. Yumaguzino		No data		6,148	4	0.07	14,359	1	0.01	5,802	0	0.00	26,309	5	0.02
48. Zilair	5,109	1	0.02	1,129	0	0.00	9,530	0	0.00	10,660	0	0.00	21,319	0	0.00
49. Ziyanchurino	3,842	0	0.00	2,044	0	0.00	14,689	0	0.00	5,129	0	0.00	21,862	0	0.00
TOTAL	92,976	25,880	27.83	253,050	120,300	47.54	548,075	254,368	46.41	254,370	117,765	46.14	1,055,495	492,433	46.65

what higher than it is farther away, but this cannot be conclusively demonstrated.

DISTRIBUTION OF BLACK HAMSTERS IN THE BASHKIRIAN A.S.S.R.

Data on the total numbers of hamsters and the numbers of black hamsters trapped in different administrative districts of the Bashkirian A.S.S.R. during the summer of 1933 and the years 1937–1939 are summarized in table 4. In spite of the fact that different districts are characterized by very different frequencies of black hamsters, the frequency of melanics in each individual district remains fairly constant from year to year. The correlation coefficient

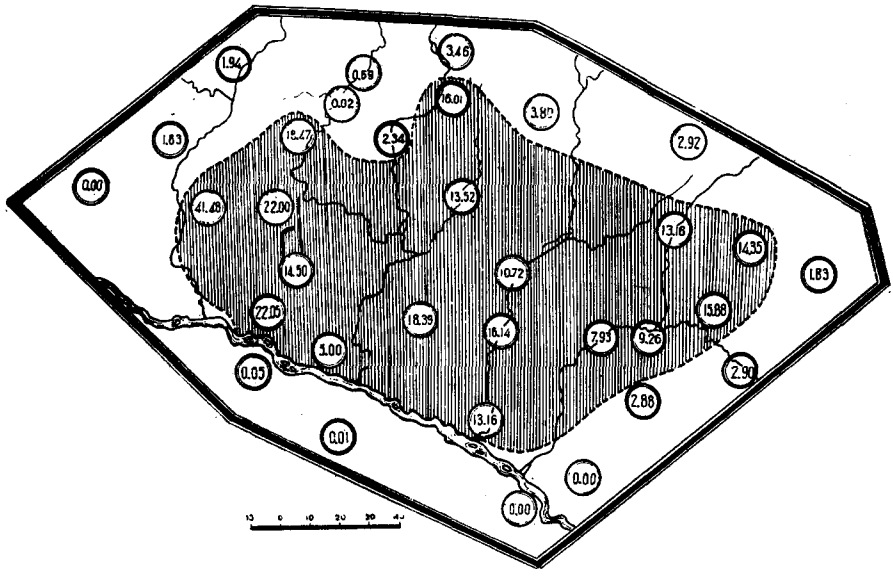

FIGURE 3. The Poltava zone of high frequency of melanics. Circles—frequency of melanics in percentage. Scale in kilometers.

between the frequencies of black hamsters in the same districts on successive years is $+0.99 \pm 0.04$. The constancy from year to year in Bashkiria, therefore, is even higher than it is in the Ukraine.

The geographic distribution of black hamsters in Bashkiria is shown in figure 4 on the basis of the average frequencies for 1937–1939 given in table 4. Black hamsters occur throughout Bashkiria with the exception of the southeastern part. The distribution area of the melanics is continuous, though their frequencies vary greatly in different localities within this area. The districts with over 60 per cent of black hamsters lie together, forming a compact zone. This zone is surrounded by a few districts with intermediate percentages (20–60 per cent), beyond which lie the districts with relatively low frequencies of melanics.

Aside from the data summarized in figure 4, data were also available concerning hamster pelts purchased by 41 district factories from May to August 1933; seven of these factories, located chiefly in western Bashkiria, are not repre-

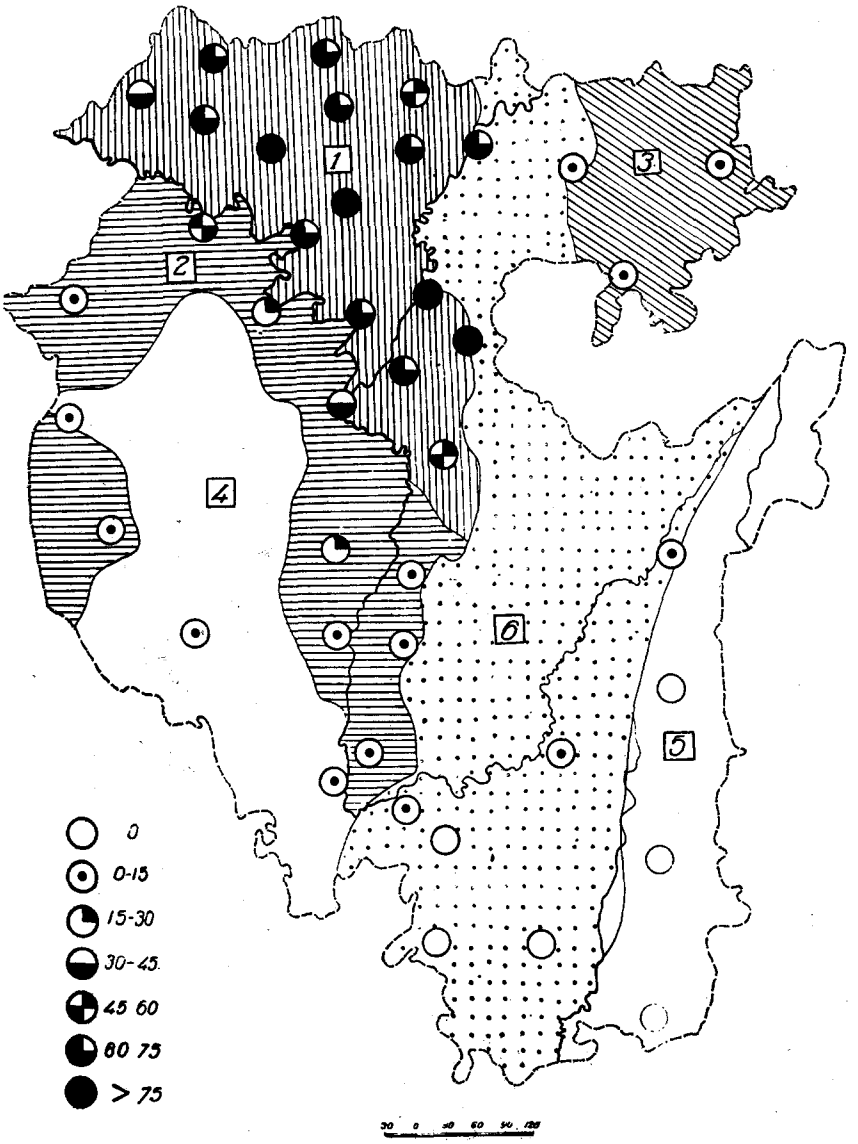

FIGURE 4. Distribution of black hamsters in the Bashkirian A.S.S.R. in 1937–1939. 1—humid forest-steppe region; 2—dry forest-steppe region; 3—mountain forest-steppe region; 4—Pre-Ural steppe region; 5—Trans-Ural steppe region; 6—mountain forest region. Circles—percentage of melanics. Scale in kilometers.

sented in the data for 1937–1939. Since, as shown in the following communication, the frequency of black hamsters is subject to some seasonal fluctuations, the data for 1933 collected during the summer months only are not fully comparable with the data for the years 1937–1939. However, the general features of the distribution of black hamsters can be ascertained even on the basis of data for a part of the year only. Figure 5 shows that all main features of the

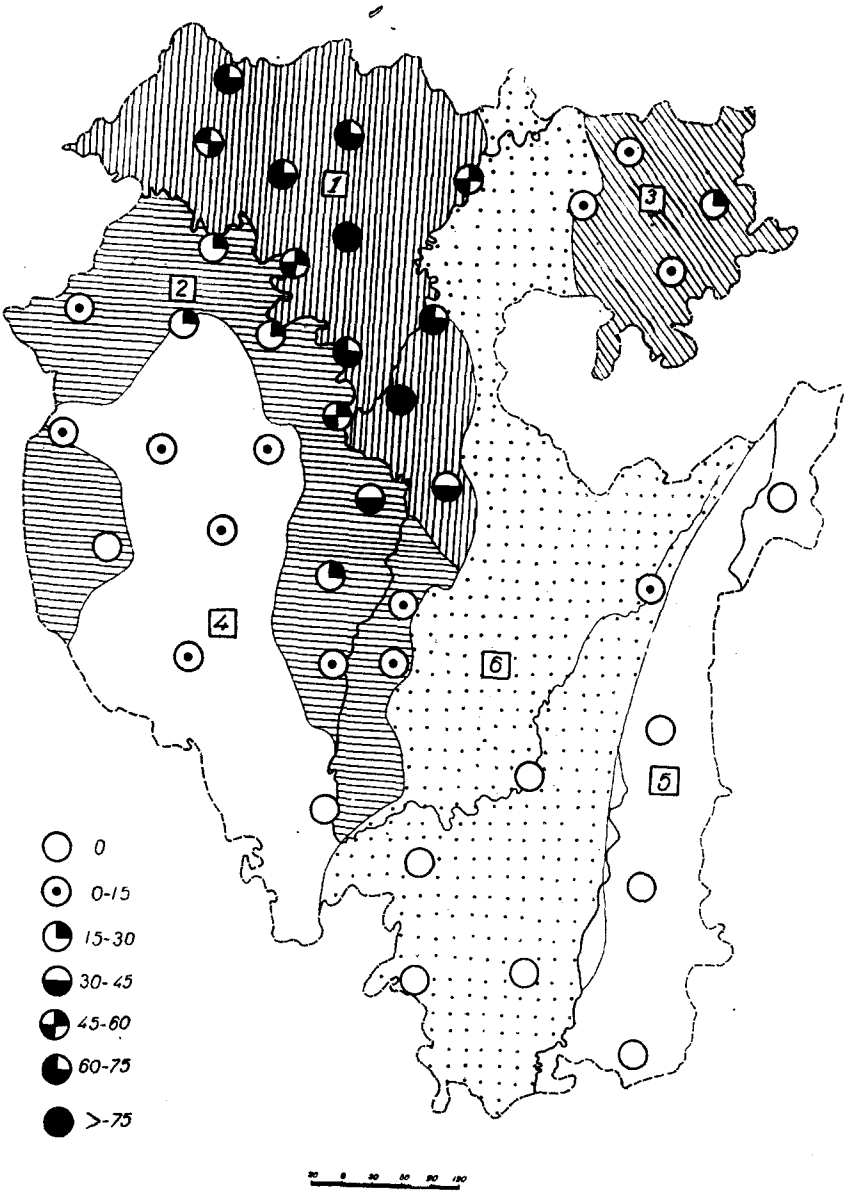

FIGURE 5. Distribution of black hamsters in the Bashkirian A.S.S.R. in the summer of 1933. Designations as in figure 4. Scale in kilometers.

distribution of black hamsters in 1933 coincide with what was observed in 1937–1939. It should be noted that these data are in good accord also with the more fragmentary information of KIRIKOV (1934) and DIAKONOV and SULLA (1935).

The types of distribution shown by black hamsters in Bashkiria and the Ukraine have much in common. In both areas black hamsters are met within

a large portion of the species distribution range, and the areas where the melanics occur are in the main continuous. The points where black individuals are particularly frequent are in both cases concentrated in discrete zones. The boundaries of these zones are generally well defined. Thus, between Karaidel and Duvan (60 kilometers) the frequency of black hamsters falls from 64 to 10 per cent, and between Iglino and Ufa from 70 to 37 per cent in less than 30 kilometers. The distribution of black hamsters in Bashkiria differs, however, from that in the Ukraine in two respects. First, the frequencies of the melanics are on the whole much higher in Bashkiria. Secondly, the zone of the high frequencies is surrounded in Bashkiria by several districts with intermediate frequencies of melanics, whereas in the Ukraine such gradients either do not exist or are but weakly pronounced.

CAUSES OF THE EXISTENCE OF BLACK HAMSTERS IN SOME PARTS OF THE UKRAINE AND THEIR ABSENCE IN OTHER PARTS

Black hamsters are present in some and absent in other parts of their distribution region in the Ukraine. This evidently cannot be explained by chance fluctuations in the reproduction and survival of the two types of hamsters, since in such a case the distribution of melanics over the vast territory where they are found could not be continuous. Three other possible explanations may be advanced. First, it can be supposed that the black mutation of the hamster, having arisen somewhere inside the investigated territory or having penetrated therein from the outside, is gradually spreading (diffusing) from its point of origin over the area of distribution of the species, but as yet has not had enough time to spread over the whole of it. Secondly, the limited distribution of melanism in only a part of the area occupied by the species can depend upon the isolation of the populations of hamsters in which melanism is present from other populations of the species. Thirdly, the ecological conditions in the regions where black hamsters are distributed may be favorable for them, whereas such conditions in other regions may be unfavorable, and consequently natural selection prevents the spread of the melanic form over the whole area of the species. Since these factors (diffusion, isolation, and natural selection) do not exclude each other, it may be that the distribution of black hamsters in the Ukraine is due to joint action of them all.

However, a number of considerations lead to the conclusion that diffusion and isolation have played at most a very insignificant part in limiting the distribution of black hamsters in the Ukrainian S.S.R. In the first place, the melanic mutation of the hamster is capable of spreading very rapidly under favorable conditions, because of the high reproductive rate of the hamster and because migrations frequently occur in this species (NOVIKOV 1933, 1935). As will be shown later in this report, the boundary of the distribution of black hamsters in the Odessa region during the time of this study was undergoing a rapid displacement southward at a rate of about 30 km per annum. So, if a diffusion of the melanic mutation could occur freely, it should have spread over all the area of distribution of the species. However, this did not take place.

Moreover, it can be shown that in at least some parts of the area of distribution of the species in the Ukraine either no such expansion occurred of the region where melanics are found or its rate was in any case very slow. As has been already mentioned, black hamsters were found by KESSLER near Zolotonosha (Poltava region) in the middle of the 19th century. At present, after a lapse of nearly a hundred years, the boundary of the area of distribution of melanics lies at a distance of only 80 km from Zolotonosha. In other words, during the whole period since KESSLER'S collections were made the territory occupied by black hamsters either remained in this part of the Ukraine without changes or at most underwent only an insignificant expansion. The absence of any gradient in the frequency of black hamsters in those regions of the Ukraine where they exist also speaks against a free diffusion of the melanic mutation from a definite center of origin.

It is also difficult to explain the absence of black hamsters in some parts of the area of the distribution of the species in the Ukraine by isolation of the populations inhabiting these parts from the populations of the regions where melanic hamsters are present. In the case of the hamsters, the role of isolating factors can be played by continuous and sufficiently wide spaces which are unsuitable for the life of this species or by such natural barriers as marshes, large surfaces of water, or mountain ranges. The data collected from hundreds of factories densely covering all the parts of the territory studied at this time show that hamsters are present throughout, with the possible exception of only the most northern part of the Zhitomir region, where lies the northern boundary of the distribution of the species. Thus, no large spaces exist in the Ukraine which are unsuitable for hamsters. Neither are natural barriers such as marshes, large surfaces of water, or mountain ranges present to separate the area where black hamsters are found from the surrounding territory. The only possible isolating factors which exist here are rivers. However, it is highly improbable that rivers may be responsible for the absence of black hamsters in some parts of the investigated territory. First of all, as may be seen in figure 1, the boundaries separating the districts where melanics are present from those where they are absent lie chiefly latitudinally, whereas the main rivers flow longitudinally. Furthermore, a detailed examination of these boundaries shows that they nowhere even roughly coincide with the large rivers. These boundaries cross a number of large rivers, as Dnieper, Desna, and Southern Bug. Literature data show that rivers in general cannot serve as effective obstacles for migration of hamsters. DUPON (1932), who studied the ways by which hamsters penetrated into Belgium, showed that in their westward movement they crossed the Rhine in historic times, and that at the end of the 19th and in the beginning of the present century they crossed a number of other rivers (for example, the Maas) and canals. NOVIKOV (1935) cites the statement of DUKELSKAIA that between 1930 and 1935 hamsters crossed the Yenisei which formed the eastern boundary of the species, and that during the several following years they populated the Minusinsk steppe lying some hundred kilometers to the east. It is known that hamsters swim well. Moreover, they fre-

quently wake from their winter sleep and run about, sometimes crossing frozen rivers during their peregrinations. Taking all this into consideration, we must agree with NOVIKOV (1935) who says that even such a large river as the Dnieper cannot serve as an isolating barrier for hamsters.

Thus, only the third explanation remains—namely, that ecological conditions in some parts of the investigated territory favor black hamsters, whereas in other parts these conditions are unfavorable. This assumption could be regarded as sufficiently well grounded only if it could be shown that such differences in the ecological conditions actually exist and that the boundary dividing the two ecological zones coincides more or less closely with that of the main area of distribution of black hamsters.

A careful comparison of the distribution of black hamsters in the Ukrainian S.S.R. with the maps of mean monthly and annual temperatures, of rainfall, and of soil, and geobotanical maps of the corresponding parts of the Ukrainian S.S.R., showed that the southern boundary of the distribution of black hamsters roughly coincides with the line separating the southern dry districts of the Ukraine (with an annual amount of precipitations less than 500 mm) from the northern more humid districts. Moreover, the area of distribution of black hamsters more or less coincides with the zone of degraded black soils; and lastly there is a close correlation between the distribution of black hamsters and the distribution of the forest-steppe vegetation. No clear connection was detected with other factors (temperature, snow-cover).

The most thorough geobotanical study of the Ukraine is that of LAVRENKO and POGREBNIAK (1930). On the basis of their descriptions of the botanical districts of the Ukraine and the map accompanying their paper, a fair picture of the limits of the zone of forest-steppe vegetation in the Ukrainian S.S.R. can be formed. As seen from the map in figure 1, the boundaries of the forest-steppe zone coincide fairly closely with the boundaries of the area of distribution of melanic hamsters in the Ukrainian S.S.R. This coincidence is more or less conspicuously disturbed only in three places: in the Zhitomir region the boundary of the area of distribution of black hamsters lies northward of the forest-steppe zone, and in the Odessa region and in the eastern part of the Kiev region it lies southward of the boundary of the forest-steppe zone. It should be noted, however, that the first two discrepancies are of very recent origin. In both cases the expanison of black hamsters beyond the forest-steppe zone occurred only during the last five or six years.

The opinion is frequently expressed that forms deviating from type are especially frequent near the borders of the distribution area of a species, where the latter meets with atypical environmental conditions (see, for example, REINIG 1938). However, in the case of melanic hamsters the situation seems to be reversed. The forest-steppe zone to which black hamsters are (at least in the Ukraine) confined is optimal for hamsters in general. This fits well with the observations of PETZSCH (1936) that the frequency of black hamsters is especially high in years when hamsters are numerous and falls when their number diminishes. In order to test these conclusions further, an attempt was made

to ascertain whether or not there is a connection between the existence of melanics and the population density of hamsters. Though the data of "Soiuspushnina" do not allow one to estimate the absolute number of hamsters inhabiting a given region or district, they give a rather precise picture of the relative density of the species. The great number of district factories, each

TABLE 5

Relative density of population of hamsters and frequency of melanics in some regions during 1935–1938.

REGION	PELTS PURCHASED PER ANNUM PER km²	PERCENTAGE OF MELANICS
Kamenets-Podolsk	3.35	4.91
Poltava	1.07	7.80
Voroshilovgrad	0.04	0.04
Zaporozhie	0.10	0.01

purchasing pelts from dozens of trappers, tends to cancel the random fluctuations in the activities of individual trappers.

Among the 15 administrative regions of the Ukrainian S.S.R. observed in this study black hamsters are practically absent in two (Voroshilovgrad and Zaporozhie), and in two others are found nearly everywhere (Kamenets-Podolsk and Poltava). Table 5 shows the average number of hamster pelts purchased in these regions per square kilometer per year during the period 1935–1938 and the average percentage of melanics among them.

TABLE 6

Relative density of population of hamsters in districts where melanics were present and where they were absent in 1938.

REGION	DISTRICTS WHERE MELANICS WERE TRAPPED IN 1938		DISTRICTS WHERE NO MELANICS WERE TRAPPED IN 1938	
	NUMBER OF DISTRICTS	PELTS PURCHASED PER km² PER YEAR	NUMBER OF DISTRICTS	PELTS PURCHASED PER km² PER YEAR
Kamenets-Podolsk	28	4.10	5	1.45
Chernigov	15	6.34	16	5.09
Vinnitsa	6	2.01	26	1.40
Odessa	9	0.94	17	0.48

The density of population of hamsters is much higher in regions lying entirely within the area of distribution of melanics than in regions where black hamsters are rare or absent. The same regularity is seen within each region if we compare districts where melanics are present with those where they are absent. This is shown in table 6. Only districts where more than one hundred pelts were purchased in 1938 are included in this table.

The density of the population of hamsters is considerably higher in districts where melanics were found than in ones where they were absent in all four regions. A similar picture is observed in other regions of the investigated territory. Thus, the conclusion that the melanic form is favored especially in such localities where the conditions are optimal for the species in general seems to be warranted.

CAUSES OF THE DIFFERENT FREQUENCY OF BLACK HAMSTERS IN DIFFERENT LOCALITIES WITHIN THE MAIN AREA OF THEIR DISTRIBUTION IN THE UKRAINE

The variation in the frequency of black hamsters in individual districts due to sampling errors must be rather insignificant, since our material includes from one hundred to several thousands of pelts purchased annually in each of the district factories the records of which served for our analysis.

The analysis of the causes of the presence of melanic hamsters in some places and their absence in others showed the existence of ecological differences between these places. If the differences in the frequency of black hamsters within the area of their distribution are conditioned by causes similar in principle, we should expect to find ecological differences also between districts with high and with low frequencies of melanics. In order to detect such differences it was necessary to make a detailed comparison of the conditions prevailing in zones of high and of low frequencies of melanics. A study was undertaken of the Chernigov zone of high frequency of melanics. Especially thoroughly studied was the eastern boundary of this zone, in the vicinity of the town of Priluki and the villages Malo-Devitsa, Rudovka, Yablonovka, Perevolochnoie, Ivanitsa, and Srebonie, where the difference between the frequency of melanics inside and outside the boundary is particularly striking. This investigation showed that the boundary of the zone of high frequency of melanics established on the basis of the data of "Soiuspushnina" coincides very closely with a line of demarcation dividing this region into parts sharply differing in their ecological conditions. Westward of this line lies a marshy lowland with soils of the black type, whereas eastward the territory is hilly, much drier, and the soils contain a large admixture of clay. The contrast between these parts is very pronounced.

Thus, the investigation of the Chernigov zone of high frequency of melanics showed that the concentration of the melanic mutation is higher in marshy districts and lower in more dry districts with a hilly relief. Though no such studies were made in other zones of high frequency of melanics, microgeographic descriptions and detailed maps of the respective districts indicate that there exist similar situations. This is also confirmed by a number of experienced trappers with whom the question has been discussed.

We have seen above that black hamsters are usually present in districts with a high density of the hamster population and absent where this density is low. A similar difference in the densities of hamster populations exists between districts with high and with low frequencies of melanics. Table 7 shows the average numbers of hamster pelts per year per square kilometer purchased during the period 1935–1938 in different regions of the territory studied, and

the average frequencies of melanics in these regions during the same period. The data for 1934 and 1939 are excluded since they do not include all the investigated regions.

The data given in table 7 confirm the conclusion that the frequency of melanics is higher in places where hamsters are more abundant. Among the 15 regions studied, three regions characterized by the highest frequencies of me-

TABLE 7

Average number of hamster pelts per year per square kilometer purchased during 1935–1938, and average frequency of melanics during the same period in different regions.

REGION	PERCENTAGE OF MELANICS	NUMBER OF PELTS PER YEAR PER km²
1. Poltava	7.80	1.97
2. Kamenets-Podolsk	4.91	3.35
3. Chernigov	4.54	3.34
4. Kharkov	3.11	0.22
5. Zhitomir	2.98	0.58
6. Stalino	1.59	0.27
7. Kiev	1.42	0.87
8. Vinnitsa	0.85	1.29
9. Sumy	0.49	0.97
10. Nikolaev	0.33	0.12
11. Dniepropetrovsk	0.24	0.68
12. Odessa	0.09	0.26
13. Kirovograd	0.05	0.61
14. Voroshilovgrad	0.04	0.04
15. Zaporozhie	0.01	0.10

lanics (Poltava, Kamenets-Podolsk, and Chernigov) occupy the first, second, and fourth places according to the density of the hamster population, whereas the three regions characterized by the lowest frequencies of melanics (Kirovograd, Voroshilovgrad, and Zaporozhie) occupy the eighth, fourteenth and fifteenth places. The coefficient of correlation between the frequency of melanics and the relative density of hamster populations, calculated on the basis of the data of table 7, equals +0.54. However, this coefficient is statistically not quite significant ($P=0.05$) because of the small number of groups into which the material is divided. Another test was therefore made of the validity of this conclusion. The coefficient of correlation between the frequency of black hamsters and the relative density of the population of the species was calculated for all the 114 districts where melanics were found in 1938 and where the number of hamsters trapped during this year exceeded one hundred. This coefficient is somewhat lower than the analogous one for regions, equalling only 0.28, but is statistically reliable ($t=3.09$).

The chief enemy of hamsters in the Ukraine is the polecat (PIDOPLICHKA 1930b); a somewhat lesser role is played by the fox, and a still lesser one by the weasel, the latter killing only the young individuals. Among birds of prey only the largest species hunt hamsters, and these species occur but rarely in the

Ukraine. The data on the frequency of black hamsters in different regions of the Ukrainian S.S.R. were compared with the data of "Soiuspushnina" on the number of polecats (*Putorius putorius* L. and *Putorius eversmanni* Lesson.), foxes, and weasels trapped in the corresponding regions. Though these data cannot characterize the absolute frequency of these predators in different regions, they probably reflect their relative frequency, since they embrace very extensive material gathered in numerous localities with many trappers and hunters. Since the administrative regions of the Ukrainian S.S.R. vary in area, the frequencies of black hamsters were compared not with the absolute numbers of polecats, foxes and weasels trapped there, but with the ratios between the numbers of hamsters and the numbers of predators trapped. Such comparisons were made for the Voroshilovgrad, Dniepropetrovsk, Poltava, Stalino, Kharkov, and most of the Kirovograd region on the basis of the data for 1938, and for the remaining regions on the basis of the data for 1939. Calculations were made of the coefficients of correlation between the frequencies of melanics and the ratios number of hamsters/number of polecats, number of hamsters/number of foxes, and number of hamsters/number of weasels. It was found that a high positive correlation exists between the frequency of melanics and the ratio number of hamsters/number of polecats ($r = +0.51$) and a lower between the frequency of melanics and the ratio number of hamsters/number of foxes ($r = +0.30$). Either no correlation exists between the frequency of melanics and the ratio number of hamsters/number of weasels or it is insignificant. Thus, black hamsters are present chiefly in such places where the number of polecats and foxes is relatively small in comparison with the number of hamsters. However, this does not necessarily mean that these predators limit the frequency of black hamsters by differentially eliminating them because of their contrasting coloration or some peculiarities of their life habits. Such a conclusion would be justified only if it were shown that the connection between the frequency of melanics and the ratio of the number of hamsters and the number of predators is not a spurious one—that is to say, is not conditioned by an uneven distribution of hamsters on the background of a more or less even distribution of predators. In order to test this possibility, the partial coefficients of correlation between the frequency of melanics and the ratios number of hamsters/number of polecats and number of hamsters/number of foxes were calculated, excluding the influence of the density of the hamster population. These calculations showed that no real correlation exists between the frequency of black hamsters and the relative frequency of polecats and foxes. On the other hand, a calculation of the partial coefficients of correlation between the frequency of melanics and the density of hamster population excluding the influence of the frequency of polecats and foxes shows that a positive correlation is here quite obvious. Therefore, it is evident that the abundance of black hamsters in localities where the environment is optimal for their species is not conditioned by a more favorable relation between the number of hamsters and the number of their natural enemies. In order to reveal the actual causes of this connection, a more detailed study of the biological differences between black and usual hamsters is necessary.

A preliminary investigation was undertaken with the purpose of finding out whether there exist in the zones of high frequency of melanics places especially favored by black hamsters or whether the animals are distributed in these zones more or less evenly. Table 8 presents the records of 26 trappers in the neighborhood of several villages in the Yablonovka district (Chernigov region) on May 3, 1941. These results were checked by the author, who was at the time present at the district factory of "Soiuspushnina."

The analysis of the data presented in table 8 does not allow a definite conclusion about the existence of real differences in the frequency of black hamsters in the vicinity of the villages studied, since these differences are statistically not quite significant, but it suggests their probability.

Further, a territory of about four km^2 near the village Yablonovka was selected and examination was made of the hamsters caught there during the

TABLE 8

Results of trapping hamsters in the vicinity of several villages in the Yablonovka district.

VILLAGE	TOTAL HAMSTERS TRAPPED	BLACK HAMSTERS TRAPPED	PERCENTAGE OF BLACK
Yablonovka	101	14	13.9
Dubovyi Gai	112	31	27.7
Bubnovshchina	59	14	23.7
Sergeievka	87	13	14.9
Rudovka	102	26	25.5
Total	461	98	21.3

11th and 12th of May, 1941, in traps placed in various micro-ecological stations. In all, 26 hamsters were caught (all adults), which were distributed as follows: on a maize field—eight normal and three black; on a mulberry plantation—three normal and one black; on an old thrashing-floor near a tobacco plantation—two normal; on a field prepared for the sowing of potatoes—five normal and four black.

It may be concluded that in the zones of high frequency of melanics black hamsters are intermingled with usual ones, though their frequency in different localities within these zones may vary rather considerably. Lastly, we must consider the four small "islands" of black hamsters which lie outside the main area of distribution of melanics in the Ukrainian S.S.R. Data about hamsters trapped there during the investigated period are given in table 9.

In the Zaporozhie and Chernigov "islands" only single black hamsters were trapped during the period studied. In the Stalino and Nikolaev "islands" black hamsters were met in considerable numbers and on the territory of two adjacent districts. The Zaporozhie "island" is separated from the main area of distribution of black hamsters by a large territory including numerous factories of "Soiuspushnina" where no melanics were recorded among many thousands of hamsters trapped during the investigated period. The possibility of the

immigration of a black individual from the main area can therefore be excluded. The Chernigov "island" lies much nearer to the main area of distribution of melanics, and the possibility of immigration of a black individual from this area is to be reckoned with. However, the absence of black hamsters in several intermediate points speaks against this possibility and makes it probable that the black individual found in this "island" also arose independently of the main area of distribution of melanics. The Nikolaev and Stalino "islands," like the Zaporozhie one, are separated from the main area of distribution of black hamsters by large territories where no melanics were found. It is

TABLE 9

Hamsters trapped in the "islands" of melanics in the Ukrainian S.S.R.

REGION WHERE THE "ISLAND" IS LOCATED	NUMBER OF DISTRICTS IN THE "ISLAND"	1934		1935		1936		1937		1938		1939		TOTAL	
		TOTAL	BLACK	TOTAL	BLACK	TOTAL	BLACK	TOTAL	BLACK	TOTAL	BLACK	TOTAL	BLACK	TOTAL	BLACK
Chernigov	1	No data		11,328	1	7,971	0	No data		11,385	0	8,274	0	38,958	1
Zaporozhie	1	447	1	181	0	356	0	127	0	126	0	No data		1,237	1
Stalino	2	11,618	765	2,198	17	4,390	29	3,202	0	698	0	No data		21,106	811
Nikolaev	2	No data		208	0	611	0	1,472	47	553	0	574	0	3,465	47

therefore also highly probable that melanism arose in these two "islands" independently of the main area. The black mutants which appeared here found conditions which allowed them to reproduce, giving a significant frequency of melanics in the corresponding populations.

CAUSES OF DIFFERENT FREQUENCIES OF BLACK HAMSTERS IN DIFFERENT DISTRICTS OF THE BASHKIRIAN A.S.S.R.

The analysis of the distribution of black hamsters in the Ukraine showed that the differences in the frequency of melanics in different localities are connected with the ecological peculiarities of the latter and are probably caused by natural selection. It seems that a similar situation exists in Bashkiria. The differences in the frequency of melanics in different parts of Bashkiria can be explained neither by accidental fluctuations in the survival and reproduction of the two investigated forms of hamsters, nor by isolation. Against the first assumption speaks the continuity of both the whole distribution area of melanics and of the zone of their high frequency. With regard to isolation, it is necessary to point out that though Bashkiria is rich in mountain ranges, some of which might possibly act as barriers for hamsters, these mountain ranges nowhere coincide with the boundaries of melanics. An analysis of detailed maps of Bashkiria shows that no other natural barriers coincide with these boundaries. The only possible exception is the western boundary of the zone of high frequency of melanics which partly (between Birsk and Ufa) coincides with the course of the river Belaia. However, since both southward and north-

ward from this region the percentages of melanics on both sides of the Belaia are very nearly equal, it is hardly probable that the differences in the frequency of black hamsters in Bashkiria are even partially conditioned by isolation.

Two possible explanations remain. Either the black mutation is more or less freely "diffusing" from some center or the differences in the frequency of black hamsters in different districts are created by natural selection. The first of these explanations is highly improbable, since black hamsters have been known in Bashkiria for over 160 years and the black mutation is capable of spreading very rapidly (GERSHENSON in press).

A detailed comparison was undertaken of the map of distribution of black hamsters in Bashkiria with topographic maps, maps of mean monthly and annual temperatures and precipitations, soil and geobotanical maps.[2] This comparison showed that black hamsters are found in Bashkiria chiefly in regions with an annual precipitation of 500 mm or higher and on degraded black soils, the situation resembling that seen in the Ukraine. Further, it was found that all the districts with a high frequency of melanics are located in the lowlands of Bashkiria (elevation less than 200 meters); in the elevated northeastern part (Ufa plateau) and southwestern part (Common Syrt) black hamsters are rare. In the southeastern part lying in the region of the Ural mountain range (elevation more than 600 meters) black hamsters are absent or rare. Finally, a connection was found between the frequency of black hamsters and the type of vegetation. The territory of the Bashkirian A.S.S.R. can be divided into the following six regions, the boundaries of which are shown in figures 4 and 5 (1) The humid forest-steppe region is characterized by a level relief, annual atmospheric precipitations of 500–550 mm, and degraded black soils. It abounds in broad-foliage woods and groves. (2) T he dry forest-steppe region intermediate between the humid forest-steppe and the steppe regions; it has a hilly relief, a smaller annual precipitation (350–400 mm), and rich black soil. Woods are scarce. (3) The mountain forest-steppe region is intermediate between the humid forest-steppe and forest regions and is located chiefly on the slopes of the smaller Pre-Ural mountain ranges. (4) The steppe Pre-Ural region is a typical level black-soil steppe region with 300–350 mm of atmospheric precipitations annually. (5) The steppe Trans-Ural region is an arid steppe region, largely with a hilly and even mountainous relief. (6) The mountain forest region is located on the Ural mountain range and on the neighboring minor mountain ranges. The extreme southwestern part of this region (between the rivers Belaia and Sakmara) is less densely covered with forests and resembles the mountain forest-steppe region.

As may be seen from figures 1 and 2, the zone of high frequency of black hamsters coincides with the humid forest-steppe region. A much lower fre-

[2] The following chief sources were used: "The Great Soviet World Atlas," Vol. I (1937), "The Ural Soviet Encyclopedia," Vol. I (1933), the official edition "The Bashkirian A.S.S.R." (1939), the works of NOVOPOKROVSKY (1931), and of IVANOV (1937) and the unpublished detailed soil and geobotanical maps of Bashkiria prepared by the BASHKIRIAN AGRICULTURAL RESEARCH STATION.

quency of black hamsters characterizes the dry forest-steppe region, and in all the other geobotanical regions of Bashkiria melanics are either rare or absent. These conclusions were further verified by three trips undertaken by the writer into the western, southern and northeastern parts of the country during which field observations on hamsters were carried out and a number of local trappers were interviewed. In Bashkiria, as in the Ukraine, black hamsters are adapted to definite ecological conditions—namely, to the forest-steppe regions and particularly to their most humid and low lying parts.

In the Ukraine the black hamsters are most frequent in localities with a high population density, where the environment is expecially favorable. To ascertain whether a similar situation exists in Bahskiria, we calculated the coefficient of correlation between the mean percentages of black hamsters in all the districts of Bashkiria and the mean numbers of hamster-pelts purchased annually per square kilometer by the local factories of the corresponding districts and found $r = +0.70 \pm 0.80$. Thus, the conclusion about the high frequency of black hamsters in places with a high density of hamster population holds for Bashkiria also. Hamsters in Bashkiria are in general more abundant than in the Ukraine, and the overall frequency of black is greater in Bashkiria.

SUMMARY

The dominant melanic form of hamster (*Cricetus cricetus* L.) presents favorable material for studies on the mechanisms of natural selection. An analysis of the distribution of black hamsters trapped in the Ukrainian S. S. R. and in Bashkiria is reported. It is based on data concerning approximately two million hamsters trapped in the Ukraine chiefly in 1934–1939, and more than one million trapped in Bashkiria during May–August, 1933, and the years 1937–1939.

In the Ukraine, as well as in Bashkiria, black hamsters are present in only a part of the total area, and the area where the melanics occur is practically continuous. Inside the area where melanics occur there are discrete nuclei in which their frequencies are especially high. The presence of black hamsters in some and their absence in other localities cannot be explained either by chance survival, by diffusion from a center of origin, or by isolation. The geographic differentiation of the population of the hamster with respect to the frequency of the black form is most probably caused by a differential fitness of melanics in diverse ecological conditions in the different districts. This differentiation is brought about by natural selection. This view is confirmed by the fact that the boundaries of the area of distribution of black hamsters in the Ukraine coincide fairly closely with the limits of the forest-steppe vegetation. In Bashkiria, black hamsters are most frequent in the more humid forest-steppe region and are rare or absent in the steppe, forest, and mountain regions.

The frequency of the melanics is correlated positively with the density of the total hamster population. No connection was found between the frequency of black hamsters and the abundance of their principal mammalian enemies.

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