EVOLUTIONARY STUDIES ON THE DISTRIBUTION AND DYNAMICS OF MELANISM IN THE HAMSTER (CRICETUS CRICETUS L.). II. SEASONAL AND ANNUAL CHANGES IN THE FREQUENCY OF BLACK HAMSTERS

S. GERSHENSON

Dept. of Darwinism, Kiev State University, and Dept. of Genetics, Zoological Institute of the Academy of Sciences of the Ukrainian S.S.R.

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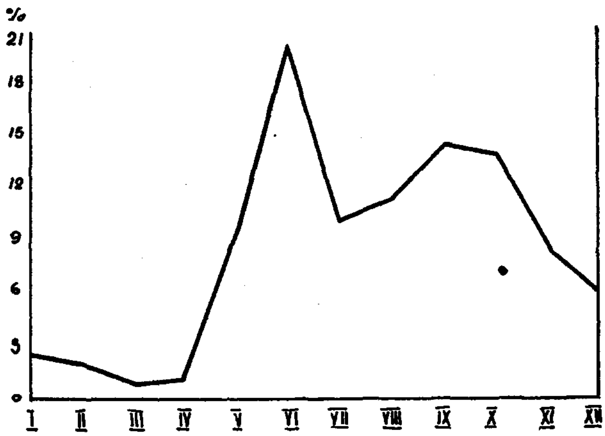
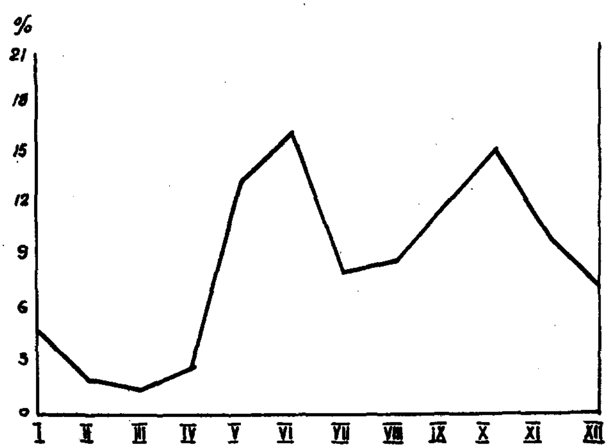
THE RECENT work of TIMOFEEFF-RESSOVSKY (1940) on dimorphic populations of Adalia, as well as the work of DOBZHANSKY (1943) and some unpublished data of our laboratories on wild populations of Drosophila, has shown that the composition of wild populations may undergo variations from season to season, these variations being conditioned by seasonal changes in the adaptive value of the genetic variants present in the population. Seasonal fluctuations in the dimorphic populations of the hamster (*Cricetus cricetus* L.) are reported in the present article. Although extensive data (GERSHENSON 1945) on the frequencies of black hamsters in various regions of the Ukraine and Bashkiria show these frequencies to be more or less constant, from year to year, nevertheless a detailed analysis of the data reveals significant alterations, more pronounced in some than in other parts of the distribution area. Since the frequency of black hamsters is controlled primarily by natural selection, a study of these seasonal and annual changes may be used to obtain an idea about the activity of natural selection in the species under consideration.

MATERIALS AND METHODS

We had at our disposal the data of fur factories of "Soiuspushnina" concerning the numbers of hamster pelts purchased monthly in some regions of the Ukrainian S. S. R. in 1936–1939, and in all of Bashkiria during 1937–1939 (GERSHENSON 1945). Only a part of this mass of data however, was suitable for examination of the seasonal changes in the frequencies of the black hamsters—namely data in which the total numbers of hamsters trapped each month and the numbers of blacks among them are sufficiently high to avoid statistical errors that might lead to erroneous conclusions. These requirements are met by the data for the Poltava, Chernigov, and Kamenets-Podolsk regions of the Ukraine and for Bashkiria. The data for Poltava region covered the period from the beginning of 1935 to the end of 1938, for Chernigov from the middle of 1935 to the end of 1939, and for Kamenets-Podolsk and for Bashkiria from the beginning of 1937 to the end of 1939.

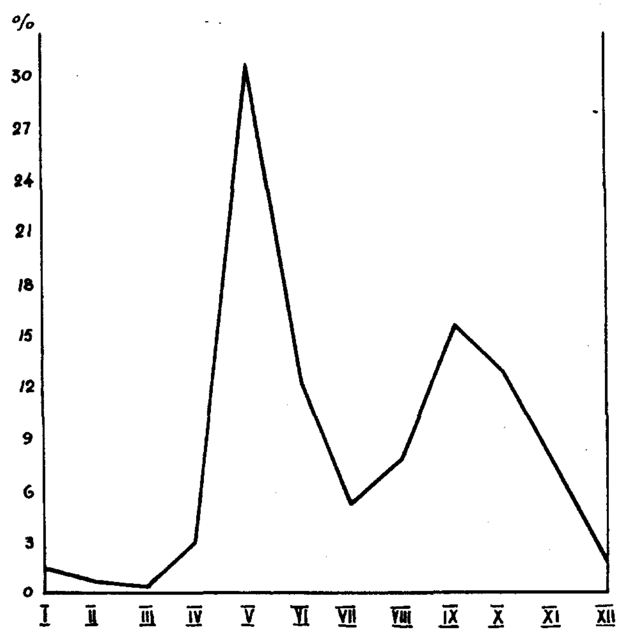
It is evidently necessary to know how much time elapses on the average between trapping the hamsters and selling their pelts to the factories of "Soiuspushnina." Two ways were used to solve this problem, namely a questionnaire was distributed among a large number of the trappers and fur agents in the territories concerned, and a study was made of the seasonal changes in the numbers of pelts purchased by the local factories of "Soiuspushnina." The answers to the questionnaire showed that hamsters are trapped in the Ukraine and in Bashkiria from the second half of April to the end of October, particularly at the beginning and at the end of this period. In midsummer, from about June 15 to August 15 in the Ukraine and from July 1 to September 1 in





FIGURES 1 and 2. Seasonal variations in the numbers of hamster pelts purchased by the district factories in various regions. The curves show mean numbers of pelts purchased during each month in percentage of the total number of pelts purchased during the whole year. Figure 1 (above).—Poltava region in 1935–1938 (total number of pelts 147,461). Figure 2 (below).—Chernigov region in 1935–1939 (total 579,355).

Bashkiria, relatively fe.re hamsters are trapped because their favorite habitats, the cultivated fields, a : inaccessible, and because most of the trappers are occupied by agricultural work. Furthermore, hamster pelts in summer are of inferior quality and are sold at lower prices. The pelts are sold usually within a month from trapping, except those trapped in autumn. However, even the



FIGURES 3 (above) and 4 (below). Seasonal variations in the numbers of hamster pelts purchased by the district factories in the Kamenets-Podolsk region in 1937–1939 (total pelts 216,157) and in Bashkiria in 1937–1939 (total 1,055,495), respectively.

autumn pelts are almost always sold before the beginning of the spring trapping season, so that little overlapping of the seasons takes place in the receipt of the pelts by the factories.

The data on the numbers of hamster pelts bought by the district factories of "Soiuspushnina" in different months of the year are summarized in figures 1–4. The seasonal variations are in all important respects similar in all the regions of the Ukraine from which data are available as well as in Bashkiria. Relatively few pelts are sold to the factories from January to March; these are the pelts obtained in autumn, the selling of which was delayed. In April the number of pelts remains low, though it is somewhat higher than in March; this is probably explained by admixture of fresh pelts obtained from spring trapping which begins in this month. In May and June the numbers of pelts rise very sharply owing to the full development of trapping. A decrease in July and August is caused by less extensive trapping during the summer months. Finally, the number of pelts increases again in September and October, and

TABLE 1

Seasonal fluctuations in the frequency of black hamsters in Poltava region in 1935–1938.

YEARS	MONTHS	TOTAL HAMSTERS	BLACK HAMSTERS	PERCENTAGE OF BLACK
	I–IV	1,339	394	29.42±1.26
	V–VI	7,397	1,187	16.05±0.42
1935	VII–VIII	4,264	438	10.27±0.47
	IX–X	4,531	504	11.12±0.49
	XI–IV	4,501	658	14.62±0.53
	V–VI	7,639	612	8.01±0.31
1936	VII–VIII	7,418	492	6.63±0.29
	XI–X	7,817	665	8.51±0.32
	XI–IV	7,875	884	11.23±0.35
	V–VI	16,748	1,343	8.02±0.21
1937	VII–VIII	9,411	327	3.47±0.19
	IX–X	14,198	774	5.45±0.19
	XI–IV	9,986	843	8.44±0.28
	V–VI	12,300	614	4.99±0.20
1938	VII–VIII	9,646	283	2.93±0.17
	XI–X	15,518	750	4.83±0.17
	XI–XII	5,973	421	7.05±0.33

drops sharply at the end of the trapping season in November and December.

The results of the questionnaire and the study of the seasonal dynamics of the numbers of hamster pelts purchased by the fur factories agree quite well. On the basis of these results, we divided the records of the district factories into the following four groups: (1) May–June, (2) July–August, (3) September–October, (4) November–April of the next year. The data for the first period reflect fairly accurately the results of the spring trapping; the few autumn pelts which in rare cases are included into the data for May may safely be disregarded, since they are very few compared to the pelts obtained in spring. The data for the second and the third periods are less exact since they reflect not only the results of the corresponding months but also include admixtures of pelts obtained earlier in the year. The data for the fourth period reflect nearly exclusively the results of the last months of the trapping season.

SEASONAL FLUCTUATIONS IN THE FREQUENCY OF BLACK HAMSTERS IN THE UKRAINIAN S.S.R.

Table 1 and figure 5 contain the data on the seasonal fluctuations of the frequency of black hamsters in the Poltava region of the Ukrainian S.S.R. in 1935–1938.

The percentage of melanics among hamsters trapped in this region is subject to very considerable seasonal fluctuations, the nature of which remains constant from year to year. Every year the percentage of black hamsters falls in winter, so that their frequency in spring is lower than in the previous autumn. A less marked decrease of the frequency of melanics continues during spring and the first half of summer, and reaches its minimum in July–August, after which a moderate increase takes place during the autumn months. These seasonal differences are statistically significant.

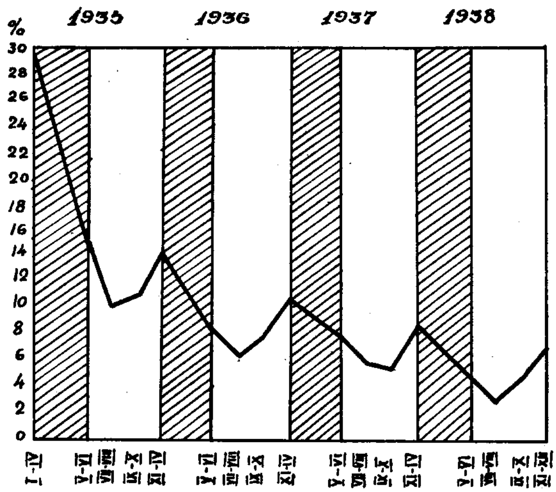
The data show that under the conditions existing in the Poltava region the relative fitness of melanics is different at different seasons of the year. Obviously, in winter the mortality of melanics is higher than the mortality of usual hamsters. The decrease in the frequency of melanics during winter can be explained only by differential elimination, no reproduction taking place during this season. If the viability of usual hamsters during the winter period be taken as unity, then the viability of melanics will be 0.44 for the winter of 1934–35, 0.51 for the winter of 1935–36, 0.69 for the winter of 1936–37, and 0.56 for the winter of 1937–38.

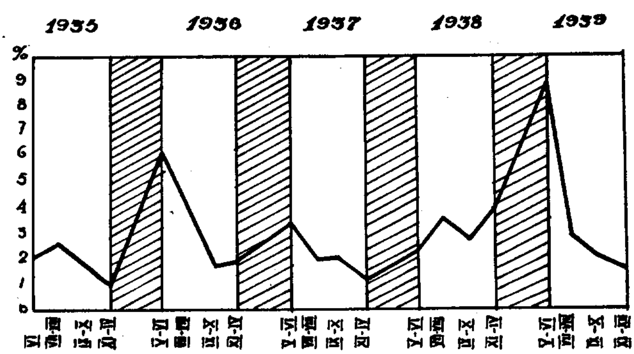
The decrease in the frequency of the melanics in July and August may be either real or only apparent. In spring and in autumn hamsters are trapped wherever they can be found, while in summer practically no trapping is done on cultivated fields. Though no data are available showing that the percentage of melanics is higher on cultivated fields than elsewhere, this possibility is not excluded. The decrease in the proportion of black pelts among hamster pelts bought by the district factories in July and August might be caused by the trapping of hamsters chiefly in such habitats where melanics are comparatively less frequent.

Quite different from the seasonal variations in the Poltava region are those in the Chernigov region (table 2 and fig. 6). Here the frequencies increase every winter. This can be explained only by a lower winter mortality of black as compared with that of usual hamsters. If the viability of usual hamsters during the winter period be taken as unity, then the viability of melanics will be 7.05 for the winter of 1935–36, 2.05 for the winter of 1936–37, 1.95 for the winter of 1937–38, and 2.50 for the winter of 1938–39. The fluctuations of the frequency of black hamsters in summer are less regular. In four out of the five years studied, a decrease in the frequency of melanics occurred in summer and autumn months, but in the summer of 1938 it was somewhat increased.

Data about the seasonal fluctuations of the frequency of black hamsters in the Kamenets-Podolsk region are given in table 3 and in figure 7.

In winter a rather considerable increase in the frequency of melanics takes place, caused by their lower relative winter mortality. If the viability of usual hamsters during the winter period be taken as unity, then the viability of melanics will be 2.11 for the winter of 1936–37, 1.11 for the winter of 1937–38, and 1.16 for the winter of 1938–39. In summer the frequency of melanics in the Kamenets-Podolsk region somewhat decreases, as it does in the Chernigov region. A feature not seen in Chernigov is a rather pronounced drop in the

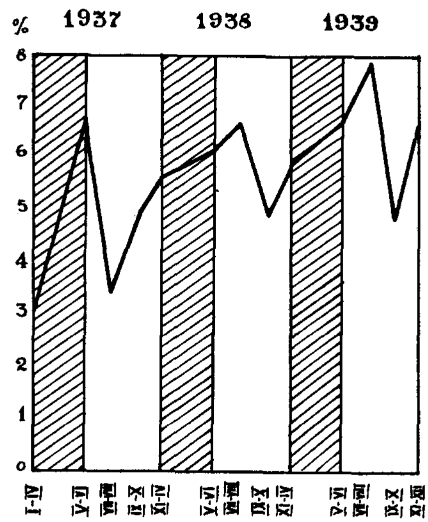


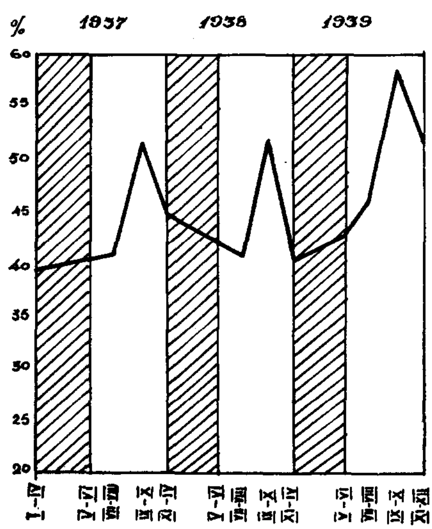


FIGURES 5 (above) and 6 (below). Seasonal fluctuations in the frequencies of black hamsters. Shaded columns indicate the winter periods. Figure 5.—Poltava region. Figure 6.—Chernigov region.

frequency of black hamsters in Kamenets-Podolsk in September–October, counterbalanced by an increase in their frequency in the following months.

Summarizing the data on the seasonal fluctuations of the frequency of black hamsters in the Ukrainian S.S.R., it is seen that in all regions from which such data were available these fluctuations are considerable and fairly regular. Most characteristic are the changes which take place in winter. In the Chernigov and Kamenets-Podolsk regions, where a continuous general increase in





FIGURES 7 (above) and 8 (below). Seasonal fluctuations in the frequencies of black hamsters. Shaded columns indicate the winter periods. Figure 7.—Kamenets-Podolsk region. Figure 8.—Bashkiria.

the frequency of melanics took place during the period studied (see below), this increase was caused by a lower relative winter mortality of melanics. In the Poltava region, where, during the period studied, the general frequency of melanics continuously decreased, this was caused by a higher relative winter mortality of the melanics. The summer changes of the frequency of melanics

TABLE 2

Seasonal fluctuations of the frequency of black hamsters in the Chernigov region in 1935–1939.

YEARS	MONTHS	TOTAL HAMSTERS	BLACK HAMSTERS	PERCENTAGE OF BLACK
	VI	20,257	396	1.95±0.10
1935	VII–VIII	17,098	396	2.32±0.11
	IX–X	23,216	386	1.66±0.09
	XI–IV	14,859	143	0.96±0.08
	V–VI	20,185	1,293	6.41±0.28
1936	VII–VIII	13,801	543	3.93±0.17
	IX–X	24,417	392	1.61±0.09
	XI–IV	19,412	351	1.81±0.10
	V–VI	15,526	550	3.54±0.18
1937	VII–VIII	12,379	268	2.16±0.13
	IX–X	38,772	797	2.06±0.07
	XI–IV	31,538	369	1.17±0.06
	V–VI	33,192	747	2.25±0.08
1938	VII–VIII	25,096	931	3.71±0.12
	IX–X	62,351	1,758	2.82±0.07
	XI–IV	6,808	2,532	3.69±0.08
	V–VI	69,894	6,110	8.74±0.11
1939	VII–VIII	38,078	1,178	3.09±0.09
	IX–X	23,061	535	2.32±0.09
	XI–XII	7,615	138	1.81±0.16

TABLE 3

Seasonal fluctuations of the frequency of black hamsters in the Kamenets-Podolsk region in 1937–1939.

YEARS	MONTHS	TOTAL HAMSTERS	BLACK HAMSTERS	PERCENTAGE OF BLACK
	I–IV	14,769	452	3.06±0.014
	V–VI	15,470	1,030	6.66±0.20
1937	VII–VIII	18,434	625	3.39±0.14
	IX–X	30,966	1,517	4.90±0.12
	XI–IV	17,330	969	5.59±0.016
	V–VI	6,958	428	6.15±0.28
1938	VII–VIII	7,511	495	6.59±0.29
	IX–X	30,633	1,512	4.94±0.12
	IX–IV	25,700	1,528	5.95±0.15
	V–VI	14,314	960	6.71±0.21
1939	VII–VIII	12,230	954	7.80±0.25
	IX–X	13,678	667	4.88±0.19
	XI–XII	8,164	558	6.83±0.28

were on the whole less regular than the winter ones; as a rule these changes occur in a direction opposite to that of the changes taking place in winter.

SEASONAL FLUCTUATIONS IN THE FREQUENCY OF BLACK HAMSTERS IN THE BASHKIRIAN A.S.S.R.

Data about seasonal fluctuations of the frequency of black hamsters in Bashkiria are presented in table 4 and in figure 8. The fluctuations here differ considerably from those observed in the Ukraine. In the winters of 1936–37 and 1938–39 the percentage of black hamsters somewhat increased, whereas in the winter of 1937–38 it decreased slightly. The relative viability of melanics is 1.11

TABLE 4

Seasonal fluctuations of the frequency of black hamsters in the Bashkirian A.S.S.R.

YEARS	MONTHS	TOTAL HAMSTERS	BLACK HAMSTERS	PERCENTAGE OF BLACK
	I–IV	7,701	2,981	38.71±0.60
1937	V–VI	78,041	31,080	41.11±0.17
	VII–VIII	10,216	4,515	42.24±0.49
	IX–X	105,238	56,357	53.53±0.15
	XI–IV	79,372	35,863	45.18±0.18
	V–VI	182,652	80,398	44.02±1.12
1938	VII–VIII	109,548	45,885	41.89±0.15
	IX–X	183,554	97,922	53.35±0.12
	XI–IV	64,261	26,483	41.21±0.19
	V–VI	195,887	89,582	45.73±0.11
1939	VII–VIII	15,314	7,249	47.34±0.40
	IX–X	19,545	11,199	57.30±0.37
	XI–IV	4,040	2,140	53.19±0.78

for the winter of 1936–37, 0.98 for the winter of 1937–38, and 1.20 for the winter of 1938–39. During most of the spring and summer months the frequency of melanics varies more or less irregularly, but an increase takes place at the end of every summer, which is followed by a drop in autumn.

An analysis of the seasonal fluctuations in Bashkiria shows clearly how cautious one must be in determining the intensity and direction of natural selection on the basis of mean annual data. In the Poltava, Chernigov, and Kamenets-Podolsk regions of the Ukraine the relative numbers of hamster pelts purchased by the fur factories during each of the periods into which the year has been divided remain more or less constant from year to year. Not so in Bashkiria. The relative numbers of hamster pelts purchased in May–June of 1939 was very high (84 per cent of all the pelts purchased during this year) as compared with the numbers of pelts purchased in the corresponding periods of 1937 (29 per cent) and of 1939 (34 per cent). Since the percentage of melanics in May–June is comparatively low in Bashkiria, this leads to a decrease in the mean annual frequency of black hamsters for 1939 (46.14 per cent of melanics as compared with 46.41 per cent in 1938 and 47.54 per cent in 1937). However, the curve shown in figure 8, as well as a comparison of the data for 1937–1939 with the data on the frequency of melanics in Bashkiria in 1933 (GERSHENSON, in press), leads to the conclusion that this decrease in the frequency of melanics in Bashkiria is only apparent and that in reality a rather rapid increase in their frequency was taking place during this period.

GENERAL TRENDS IN THE FREQUENCIES OF BLACK HAMSTERS IN THE UKRAINE

The data on the frequencies of black hamsters in different regions and districts of the Ukrainian S.S.R. (GERSHENSON 1945) show that these frequencies do not remain absolutely constant from year to year but show some significant changes. Furthermore, it is noteworthy that in some parts of the Ukraine a general increase and in other parts a decrease was observed. The first of these tendencies predominates, so that the frequency of black hamsters in the Ukraine taken as a whole has markedly increased during the period of observation.

If the districts in which the frequencies of black hamsters have significantly increased, decreased, or remained stationary are plotted on a map of the Ukraine, it becomes clear that these three classes of districts are not distributed at random but form practically continuous zones. One zone is characterized by a general increase, another by a decrease, whereas the relatively few districts which showed a constant frequency of black hamsters are located mostly between the first two zones. The zone in which the percentage of black hamsters increased during the period of investigation includes the Vinnitsa, Zhitomir, Kamenets-Podolsk, Kiev, and Odessa regions, parts of the Dniepropetrovsk and Kharkov regions, and small parts of the Sumy and Poltava regions, thus occupying chiefly the western part of the territory studied. The other zone, characterized by the decrease in the frequency of melanics, lies entirely in the eastern part of this territory and includes the Stalino region, nearly all the Sumy and Poltava regions, and parts of the Kharkov and Dniepropetrovsk regions. Moreover, it probably includes the Voroshilovgrad region, where the frequency of melanics is too low to allow any safe conclusions.

The fact that both an increase and a decrease in the frequency of melanics characterized continuous zones leads to the supposition that each of these two tendencies is conditioned by some general factors operating over large territories. However, an examination of the annual changes in individual regions shows that these tendencies may be realized in a highly diverse fashion even in regions located closely to one another, so that, for example, in two neighboring regions, both of which are characterized by a general increase in the frequency of melanics during the period studied, the intensity and even the direction of natural selection of melanics during individual years may vary practically independently. It is thus evident that besides general factors operating on large territories and controlling the main course of natural selection, important factors of a more local type exist which determine the mode of realization of these general tendencies in each given place and at each given time. These local factors will be discussed in a later part of the present paper.

Highly noteworthy is the fact that in all the regions where a general increase in the frequency of black hamsters occurred during the investigated period, a steady extension of the area of distribution of melanics took place. This is clearly seen in figures 9 and 10, where the boundaries of the area of distribution of melanics in the Odessa and Chernigov regions respectively are shown for each of the five years studied. Especially rapid was the extension of the area of distribution of melanics in the Odessa region, where the southern boundary of this area was shifted approximately 150 kilometers southward during the period 1935–1939. A similar situation was observed also in the Vinnitsa, Kamenets-Podolsk, Kiev and Zhitomir regions. The extension of the area of distribution of melanics took place in all these regions in a "tongue-shaped" fashion—that is, the area was extended only in one or a few directions without losing its continuity. This last fact is important since it shows once more (see GERSHENSON 1945) that chance survival plays no important part in the geographical distribution of black hamsters.

In the regions where a significant general decrease in the frequency of black hamsters occurred during the investigated period, a reverse process took place —that is a reduction of the area of distribution of melanics. This may be seen especially well in the Stalino region, where melanics completely disappeared toward the end of the period of investigation; a similar change was observed also in the Sumy region, in a part of the Kharkov region, and probably in a part of the Dniepropetrovsk region. The insufficient number of factories in these regions from which statistically-significant data were available prevents as detailed an analysis of this process as it was possible to make in the cases of the extension of the area of distribution of melanics.

THE INTENSITY OF NATURAL SELECTION OF MELANICS IN DIFFERENT PARTS OF THE UKRAINE

To understand the role of natural selection in the transformation of wild populations, it is necessary to know the intensity with which it operates. Few data on the question exist in the literature, and most of the investigators who discuss the mechanisms of natural selection assume arbitrary values characterizing the intensity of natural selection, usually assuming that this intensity is very low.

We determined the intensity of natural selection of black hamsters by means of the formula proposed by HALDANE (1932)

$$k = P_{n+1} - P_n / P_{n+1} q_n^2$$

where k is the coefficient of natural selection, P_n is the concentration of the dominant allele in the n-th generation, q_n the concentration of the recessive allele in the same generation, and P_{n+1} the concentration of the dominant allele in the next generation. If the value of k is positive, it means that selection favors the dominant allele (in this case melanism); if it is negative it means

FIGURE 9. Extension of the area of distribution of black hamsters in the Odessa region in 1935–1939. Based on data from 42 factories each year.

that selection proceeds in the opposite direction. The value of k may vary between $k = +1$ and $-\infty$.

The above formula is deduced for cases when no overlapping of generations occurs. When generations overlap, as is the case in hamsters, a correction may be introduced. However, this correction holds only when the coefficient of selection is small, which is not the case in the present material, as will be

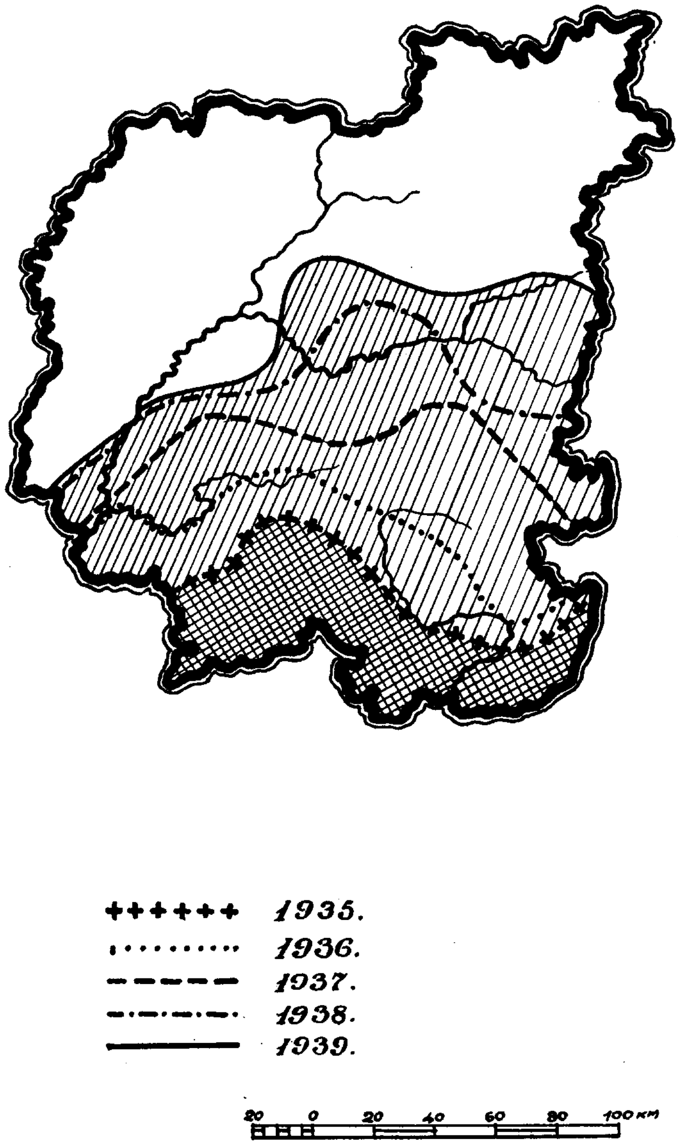


FIGURE 10. Extension of the area of distribution of black hamsters in the Chernigov region in 1935–1939. Based on data from 43 factories each year.

presently shown. Consequently, an exact determination of the values of k for the data here is impossible. All that can be done is to determine the approximate values of the coefficient of natural selection of melanics.

As was shown by PIDOPLICHKA (1928 and personal communication), hamsters reach in nature a maximum age of four to six years; this was found on the basis of a comparison of the condition of the teeth of the oldest hamsters trapped in nature with the condition of the teeth of hamsters kept in captivity whose exact age was known. There can be no doubt that very many wild hamsters perish before reaching this age limit. In calculating the coefficients of selection we may proceed from the supposition that hamsters reproduce in nature only during one year and then perish; in this case the coefficients of selection obtained will be lower than the actual ones. On the other hand, we may proceed from the supposition that hamsters reproduce in nature during the entire potential period of their life—that is, approximately during five years; in this case the coefficients of selection obtained will be higher than the actual ones. The actual coefficients of selection will lie between these minimal

TABLE 5

Minimal and maximal coefficients of natural selection of black hamsters in different regions of the Ukraine.

REGION	TOTAL NUMBER OF HAMSTERS	NUMBER OF BLACK HAMSTERS	MINIMAL COEFFICIENTS OF SELECTION					MAXIMAL COEFF. OF SELECTION
			1934–35	1935–36	1936–37	1937–38	1938–39	
Vinnitsa	155,586	1,683	No data	0.98	−0.86	0.94	0.44	0.99
Dniepropetrovsk	118,448	248	0.72	−0.32	0.81	−0.02	No data	0.75
Zhitomir	82,996	2,580	No data	0.89	−0.29	−0.34	0.39	0.89
Kamenets-Podolsk	333,002	16,140	No data	0.66	0.18	0.14	0.11	0.82
Kiev	188,127	3,180	No data	0.57	0.14	0.12	0.25	0.76
Odessa	39,700	471	No data	0.58	0.20	0.67	−0.06	0.88
Poltava	167,848	13,756	0.18	−0.56	−0.40	−0.34	No data	1.39
Stalino	41,821	1,211	−0.63	−0.52	0.79	Negative	No data	Negative
Sumy	97,371	498	−0.82	0.83	0.20	−0.24	No data	−0.31
Kharkov	32,956	903	0.72	0.30	0.11	−0.33	No data	0.76
Chernigov	582,533	19,813	No data	0.57	−0.56	0.29	0.23	0.58

and maximal values, probably somewhat nearer to the minimal ones. For the sake of brevity, the coefficients of selection calculated by the first method (comparison of adjacent years) will be designated "minimal coefficients of selection" and those calculated by the second method (for the five-year period) "maximal coefficients of selection."

In table 5 are given the minimal coefficients of selection of melanics for all the investigated regions of the Ukraine except the Zaporozhie, Voroshilovgrad, Kirovograd, and Nikolaev regions, where the frequency of melanics was too low to allow such calculations.

It is necessary to note that the coefficients of selection presented in table 5 are somewhat more nearly exact for the Kamenets-Podolsk, Kiev, Poltava, and Chernigov regions than for all others. As shown previously (GERSHENSON 1945), determination of the coefficients of selection on the basis of mean annual data is not quite exact, since the frequency of melanics is subject to marked seasonal fluctuations. The relative number of hamsters trapped in each season may vary from year to year. Therefore, for regions from which data was available on the frequency of black hamsters at different seasons—namely, for Kamenets-Podolsk (1937–1939), Kiev (1935–1939), Poltava (1935–1938) and Chernigov (1935–1939)—the mean of the frequencies of melanics at different seasons (see GERSHENSON 1945) was taken as the mean annual frequency of melanics used for the determination of the coefficients of selection. However, it should be noted that the relative number of hamsters trapped at different seasons in the Ukraine varies relatively little from year to year, so that the correction introduced by the described method is comparatively small. This may be illustrated by a comparison of the maximal coefficients of selection calculated by the more exact method (on the basis of the means of the frequencies of melanics at different seasons) for the Kamenets-Podolsk, Kiev, Poltava, and Chernigov regions with the maximal coefficients of selection for the same regions calculated by the usual method (on the basis of mean annual frequencies of melanics).

An examination of table 6 leads to two conclusions. First, it is evident that the course of natural selection is very irregular both in the regions where the frequency of melanics showed a general increase during the investigated period

TABLE 6

A comparison of the maximal coefficients of natural selection of black hamsters calculated by the more exact and by the usual methods.

REGIONS	EXACT METHOD	USUAL METHOD
Kamenets-Podolsk	0.82	0.82
Kiev	0.76	0.74
Poltava	−1.39	−1.27
Chernigov	0.58	0.66

and in those where it showed a general decrease; not only is the intensity of selection different in different years in each region, but even its direction is frequently reversed. Secondly, the coefficients of natural selection are as a rule very high. In other words, the adaptive values of the alleles of usual coloration and of melanism are highly different, this difference being equally striking both when natural selection favors the former and when it favors the latter. Out of 43 cases where we could determine the minimal coefficients of selection, in only two cases the black mutation proved to be more or less neutral (Dniepropetrovsk region 1937–38 and Odessa region 1938–39). Typical are minimal coefficients of selection (both positive and negative) of the order 0.2–0.6 and maximal coefficients of selection of the order 0.7–0.9.

As has been shown above, a general increase in the frequency of black hamsters took place during the period of investigation on a large continuous territory, including several administrative regions of the Ukraine; a somewhat smaller area where the frequency of melanics showed a general decrease during the same period was also practically continuous. It is thus evident that a natural selection of black hamsters is at least partially controlled by some factors operating over large territories. However, as we have already pointed out, there is good evidence for the existence of other factors of a more local type, as a result of the action of which the course of natural selection of melanics may considerably differ even in adjacent regions. In order to study this question we applied a method proposed by LIUBISHCHEV (1936) for a similar problem concerning the harm produced by insect pests. The coefficients of correlation between the minimal coefficients of selection of all pairs of adjacent regions[1] were determined for corresponding years during the period 1935–1938.

This coefficient of correlation proved to be only 0.25±0.13, indicating that the role of local factors controlling the course of natural selection is very important. We further tried to ascertain whether such local factors operate in territories including several adjacent administrative districts or whether their

TABLE 7

Minimal coefficients of natural selection and correlation between them in pairs of adjacent districts.

PAIRS OF DISTRICTS	MINIMAL COEFFICIENTS OF SELECTION					COEFFICIENTS OF CORRELATION
	1934–35	1935–36	1936–37	1937–38	1938–39	
Kozelshchina	−0.48	−0.50	−0.25	0.76	No data	−0.82±0.17
Kobeliaki	−0.35	0.17	−0.27	0.51	No data	
Semenovka	0.70	−1.92	0.20	0.23	No data	0.98±0.01
Khorol	0.75	−3.96	0.15	−0.23	No data	
Malaya Devitsa	No data	0.24	0.35	0.29	0.04	0.03±0.45
Priluki	No data	0.77	−0.18	0.48	0.05	
Nosovka	No data	−0.09	−1.60	0.38	−0.08	0.46±0.39
Bobrovitsa	No data	0.78	0.11	0.29	0.28	
Volochisk	No data	0.53	−0.21	0.54	−0.28	0.97±0.03
Teofipol	No data	0.21	−1.04	0.57	−0.64	

action is restricted to still smaller territories. With this aim all pairs of adjacent districts were selected from which data were available for all the five years studied and where both the total number of hamsters trapped and the frequency of melanics were high enough to enable sufficiently exact calculations. Five pairs of districts answered these requirements—two in the Poltava region (Kozelshchina-Kobeliaki, Semenovka-Khorol), two in the Chernigov region (Malaya Devitsa-Priluki, Nosovka-Bobrovitsa) and one pair in the Kamenets-Podolsk region (Volochisk-Teofipol). For each pair of districts all four minimal coefficients of selection for the corresponding years were compared and their coefficient of correlation found (table 7).

As may be seen from table 7, the correlation between the coefficients of selection of adjacent districts is in three out of five cases positive, in one case

[1] These pairs are: Vinnitsa-Zhitomir; Vinnitsa-Kamenets-Podolsk; Vinnitsa-Kiev; Vinnitsa-Odessa; Dniepropetrovsk-Poltava; Dniepropetrovsk-Stalino; Dniepropetrovsk-Kharkov; Zhitomir-Kamenets-Podolsk; Zhitomir-Kiev; Kiev-Odessa; Kiev-Poltava; Kiev-Chernigov; Poltava-Sumy; Poltava-Kharkov; Poltava-Chernigov; Stalino-Kharkov; Sumy-Kharkov and Sumy-Chernigov.

negative, and in one case absent. The fact that in two cases the positive coefficients of correlation are statistically significant and very high makes it probable that the factors controlling the intensity of natural selection of melanics are in at least some cases common to adjacent regions—that is, to territories of the order of 800–1500 square kilometers.

NATURAL SELECTION OF MELANICS IN BASHKIRIA

The percentage of melanics in Bashkiria was relatively much more constant during the period 1937–1939 than in the Ukraine. The coefficients of selection were calculated here by the more accurate method (on the basis of the mean frequencies of melanics at different seasons), since the relative numbers of hamsters trapped during different seasons varied considerably in Bashkiria. These calculations showed that the general frequency of melanics in Bashkiria increased somewhat during the period 1937–1939, though the course of natural

TABLE 8

The frequency of black hamsters in 32 districts of Bashkiria in May-August 1933 and in May-August 1937.

PERIOD	TOTAL NUMBER OF HAMSTERS	NUMBER OF BLACK HAMSTERS	PERCENTAGE OF BLACK
May-August 1933	79765	23944	30.02
May-August 1937	71908	30637	42.61

selection was erratic. If we exclude the few districts in respect to which data were not available for all three years studied, the frequency of melanics in Bashkiria becomes 45.52 per cent in 1937, 45.12 per cent in 1938, and 50.89 per cent in 1939. The corresponding minimal coefficients of selection are −0.08 for 1937–38 and 0.18 for 1938–39. The minimal coefficients of selection for individual districts in the great majority of cases are also relatively low. The highest were observed in the Ufa district (0.31 for 1937–38 and −0.49 for 1938–39), but such high values are exceptional; in many districts they are too low to be significant. The greatest increase in the frequency of melanics during 1937–1939 took place in the Diurtulli, Kaltasy, Mishkino and Krasnousolsk districts, the first three of them being adjacent. A more or less considerable decrease in the frequency of melanics occurred only in one district (Kushnarenkovo).

Besides the data for 1937–39 there were available the data of the fur factories of "Soiuspushnina" concerning the frequency of black hamsters in Bashkiria in May-August 1933. Since the frequency of black hamsters is subject to considerable seasonal fluctuations, these data may be compared only with the data for the corresponding months of other years. Data on the frequency of melanics in Bashkiria in May–August, 1933, and for the corresponding months in 1937 are presented in table 8. Only 32 districts out of the 49 studied are taken into account.

Table 8 shows that the frequency of black hamsters in Bashkiria was increasing not only in 1937–1939, but also during the preceding five years. The maximal coefficient of natural selection of melanics for these five years (1933–37) equals 0.58.

Out of 25 districts where melanics were present both in 1933 and 1937 their frequency increased significantly in 12 districts, remained more or less constant or slightly increased in ten districts, and significantly decreased in only three districts lying in the central part of Bashkiria (Iglino, Mishkino, and Ufa).

It is interesting to note that out of the four years (1933 and 1937–39) covered by this study of hamsters in Bashkiria, one year (1938) was a year of mass reproduction of hamsters (a "hamster year" according to the terminology of the fur-trade). This fact, which was pointed out by local trappers, was fully confirmed by the data on the numbers of hamster pelts purchased by the district factories during the corresponding years. The total number of hamster pelts purchased by the fur factories in Bashkiria in 1938 (548,075) is nearly double the number purchased in 1937 (253,050) or in 1939 (254,370). According to the observations of PETŽCH (1936), in years of mass reproduction of hamsters a sharp increase in the frequency of melanics takes place. Our data on the positive correlation between the frequency of black hamsters and the density of the population of the species (GERSHENSON 1945) speak in favor of the same assumption. However, in the present case not only no increase in the frequency of melanics took place in Bashkiria, but the year 1938 showed even a slight decrease in the percentage of black hamsters. It is possible that this fact could be attributed to the climatic peculiarities of that year. The winter of 1937–1938 in Bashkiria was rather mild, and this could lead to the overwintering of unusually high numbers of hamsters. On the other hand, the summer of 1938 was exceedingly dry, and this could lead to a decrease in the frequency of melanics, the latter being better adapted to humid conditions (GERSHENSON 1945). In any case, it is clear that the conclusion reached by PETZCH is by no means universal, and in studying the connection between mass reproduction of hamsters and the frequency of melanics it is necessary to take into consideration the ecological peculiarities of the respective years.

SUMMARY

The data for the Poltava, Chernigov, Kamenets-Podolsk regions of the Ukrainian S.S.R. show that the relative frequencies of black hamsters in these regions undergo regular and significant changes from season to season. In winter the frequency of black hamsters in the Poltava region decreases, and in the Chernigov and Kamenets-Podolsk regions it increases. These changes in the frequencies of black hamsters during winter are caused by their lower (or, respectively, higher) viability compared to that of normal hamsters. The changes in the frequencies of black hamsters taking place during the summer months are less regular and less rapid than those taking place in winter, but, on the whole, these summer changes occur in directions opposite to the changes which take place in winter in the same region.

In Bashkiria the frequencies of black hamsters underwent increases during the winters of 1936–37 and 1938–39, but decreased in the winter of 1937–38. At

the end of every summer a sharp increase is observed, following which a sharp decrease takes place during autumn. Taken as a whole, the seasonal variations are smaller in Bashkiria than in the Ukraine.

Aside from the above cyclic changes in the frequencies of black hamsters, some systematic changes were taking place in the territories investigated during the period 1934–1939. In the western portion of the Ukraine the frequencies of black hamsters were increasing and in the eastern portion decreasing. The increase in the incidence of the melanics was accompanied by extension of their distribution area. It is very probable that a reduction of the distribution area of the melanics occurred in the eastern regions where their frequencies were diminishing.

The course of the natural selection of the melanics was very uneven both in those parts of the Ukraine where their general frequency was rising and where it was declining. The intensity of selection varied from year to year in each region, and reversals in the direction of selection occurred from time to time. This indicates that, besides factors which determine the general trends of natural selection in large territories, an important role is played by more local influences which control the course of selection in smaller subdivisions of these territories.

A general and fairly rapid, though uneven, rise in the frequencies of black hamsters took place in Bashkiria in 1933–1939.

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