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Phenotype and gene frequencies in red fox populations of Russian America in 1803–1832

ABSTRACT: From game records of 1803–1832, distinct differences in *B* gene (Alaskan black coat color) frequencies between island and mainland red fox populations of Russian America were established. The level of polymorphism for coat color was stable during this period.

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THE RARITY of visible polymorphisms for Mendelian characters in mammals has imposed limitations on genetic studies of populations. When clearcut, polymorphisms have made it possible to analyze the geographic distribution of gene frequencies and to estimate the contribution of such factors as isolation and selection to microevolutionary processes in populations. Thus, investigations of gene distribution in the domestic cat, a species conspicuously polymorphic for some ten genes have been helpful in elucidating how evolution operates in geographically distinct localities[17]. However, the domestic cat is not a suitable tool for unraveling the genetic variability existing in natural populations, and the results obtained with this species cannot be directly applied to wider evolutionary problems. The impact of man's will and whims in the course of the domestication of the cat has been so strong that modifications of its population genetic profiles are justly regarded as anthropogenic: artificial selection for coat color has brought about changes in the frequencies of corresponding alleles and its migration has been largely subordinated to the movements of human populations[2,17].

Polymorphism for coat color controlled at a single locus has been described in the red fox (*Vulpes vulpes* L.) whose range is the Far East and Alaska. This offered a unique opportunity for surveying coat polymorphism of foxes in various sites, both in the Old and New World. Alaskan foxes homozygous for the *B* allele are black, while those homozygous for the b allele are reddish brown (red); a mixture of the two colors is observed in heterozygotes *Bb* (cross or *sivodushka* in Russian)[8,14].

In Canadian fox populations, silver-black coat color is controlled by the *R* gene[3,8]. Polymorphism for this gene has been thoroughly described[3–5,7,15,18], and a north-south gradient[4] and density dependence[5] for the frequency of this allele have been established. An annual recurring decrease in the frequency of melanics has been observed[3,7]. Haldane[7] thought this resulted from the preference of hunters for this color phase, which was valued two or threefold above any other.

The only attempt to analyze the geographic distribution of genes determining coat polymorphism in fox populations in areas of the Bering Sea basin was made by Romashov and Iljina[16]. Examination of game records of foxes in the Chukotka and Kamchatka Peninsulae and Karaginsky Island revealed that, in most samples, their phenotype frequency distribution (black, cross, and red) conformed to that predicted by the Hardy-Weinberg law. This analysis also demonstrated that the frequency of the *B* gene is much higher in island than in mainland populations. However, from the evidence available it is not clear whether the differences between the two populations are based on regular patterns or are due to chance alone.

This paper relates to the nature of the differences in gene frequencies between mainland and island fox populations. The period includes 29 years from 1803 to 1832. The study is based on the accounts of the

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management board director of the Russian American Company, the corresponding member of the Russian Imperial Academy of Sciences, K. T. Khlebnikov. These accounts have only recently appeared as a single volume[12].

Phenotypic Distribution of Wild Foxes

A particularly valuable aspect of Khlebnikov's accounts is that the phenotypic ratios of wild-caught foxes in each trader station are indicated separately. Because the foxes were captured in restricted territories, the samples representing the local populations seem reliable.

The commercial value of fox pelts varied largely depending on the color phase, and the estimates given are not total sums but represent the number of each particular color phase.

The results of the chi-square statistical analysis between the phenotypic distribution observed and the one predicted by Hardy-Weinberg equilibrium are presented in Table I. There is a significant fit for the great majority of the fox populations, and this is so noted in the table. The only discrepancy is observed for the trader stations on the islands of Unga and Hinchinbrook, but these do not detract from the general conclusion of good conformance.

Since the trader stations on Unga and Hinchinbrook Islands sent expeditions to various sites on the mainland and adjacent islands[12], the phenotypic frequencies in Table I do not represent the actual frequencies there.

Noteworthy is the slightly less than expected number of heterozygotes in many of the local samples. Romashev and Iljina[15] have also established this deficiency in Far Eastern populations. It may be due to erroneous identification of phenotypes and/or to small population number and, consequently, to disturbed panmixia. That the population size and the territories inhabited are, indeed, small is evidenced by the high heterogeneity of samples from the various traders' stations on the largest islands of the chain, Kodiak ($\chi^2 = 5.0$; $0.05 > P > 0.02$) and Unalaska ($\chi^2 = 4.5$; $0.05 > P > 0.02$).

A map of the distribution frequencies for the *B* gene in Alaska and adjacent islands is given in Figure 1. It is based on the 1824 data; 1832 data were available for the trader station in Nushagak.

It will be noted that the frequency of the *B* gene is extremely low for all the mainland populations, except in the region of Kenai Bay. The Aleutian mountain range, which rises 2,000–3,000 meters at its highest elevation, is an unsurmountable isolating barrier for this population. The frequency of the *B* gene in the Kenai population attains 0.55. Describing the wildlife, Khlebnikov[12] noted the occurrence of foxes, predominantly black and cross. The fox population inhabiting Unimak Island, which is closely adjacent to the coastline of Alaska, is similar to the population of the mainland from where it has presumably migrated.

Khlebnikov[12] also reported that Afognak Island is rich in foxes, mostly black. Indeed, from his data it follows that on this island, the frequency of the *B* gene is as high as 0.75, being the highest of all the fox populations considered. The group of Fox Islands (Unalaska, Umnak, Akun) and Kodiak Island were inhabited by foxes very similar with respect to the frequencies of the *B* alleles.

There are no comparable Nineteenth Century data for populations of the Chukotka and Kamchatka Peninsulae, nor for Komandarski and Kurile Islands. However, an overview of the more recent data (1914–1930) collected for these sites by Romashov and Iljina[16] suggests an explanation of the differences. The frequency of the *B* gene for the mainland populations (the Chukotka and Kamchatka Peninsulae) did not exceed 0.02–0.08, i.e., it was very close to the frequencies established for the mainland populations of Alaska. The frequency of the *B* gene on Karaginski Island was almost the same as that on the islands of Russian America, 0.24–0.28[16]. From analysis of more recent data, it emerged that the frequency of the *B* allele was negligibly small on the Chukotka Peninsula and Yakut territories (0.04)[14], and quite high in the Kurile Islands (0.39)[19]. It is difficult to reconcile the two observations: the discrepancy between the gene frequencies of mainland and island populations and the corresponding frequencies in island populations that are further away from the mainland.

Table I. Phenotype and gene frequencies in fox populations of Russian America in 1824

Site	Trader station	Frequencies observed† BB	Bb	bb	expected BB	Bb	bb	χ^2	P(B)
Alaska	Nushagak	1	7	121	0.2	8.6	120.2	3.5	0.04
Alaska	Katmai	—	3	111	0	2.3	111.7	0.2	0.01
Alaska	Sukhtum	—	—	62	—	—	62	0	0
Alaska	Kenai	41	49	28	36.4	57.7	23.9	2.6	0.55
Unimak Is.	Unimak	—	—	168	—	—	168	0	0
Unga Is.	Unga	39	71	546	8.4	132.1	515.5	141.6**	0.11
Hinchinbrook Is.	Hinchinbrook	5	4	25	1.4	11.2	21.4	14.5**	0.21
Afognak Is.	Afognak	62	39	8	61.0	41.1	6.9	0.3	0.75
Kodiak Is.	Igak	19	39	32	16.5	44.1	29.4	1.2	0.43
Kodiak Is.	Trekhsvyatitel'ska	59	104	89	48.9	124.1	79.0	6.6	0.44
Kodiak Is.	Alitak	37	55	47	29.9	69.2	39.9	5.9	0.46
Kodiak Is.	Karluk	62	122	63	61.3	123.5	62.2	0.1	0.50
Unalaska Is.	Harbor	68	134	71	66.8	136.6	69.6	0.1	0.49
Unalaska Is.	Makusha	23	42	43	17.9	52.2	37.9	4.1	0.41
Unalaska Is.	Koshiga	10	69	70	13.2	62.6	73.2	1.6	0.30
Akun Is.	Akun	78	124	55	76.3	127.5	53.2	0.2	0.54
Umnak Is.	Umnak	40	95	51	41.2	92.6	52.2	0.1	0.47

† This table is based on data derived from Khlebnikov[12] (p. 31, 80, 128)
** $P > 0.999$

Migration Pathways

One can envisage two migration pathways of foxes. The Alaskan coastline is never entirely blocked by ice because the waters are warmed by the Alaskan current (water temperature is 2°C in February[6]). This makes it impossible for foxes to pass over ice from the islands to the mainland and back through the Shelikhof Strait. In winter, large floating masses of ice project over the waters. Drifting, they make their way from one island to another with a rate of 1.5 km/h. These masses can serve as "maritime transport facilities" for foxes. Khlebnikov[12] has aptly noted this possibility indicating that foxes have thus reached the Fox Islands, gained access to the islands studding the ocean further west and north up to the Pribilof Islands. This has provided a steady westward flow of foxes from one island to another.

In an attempt to explain the differences in the concentrations of the *B* gene, emphasis should not be placed solely on this

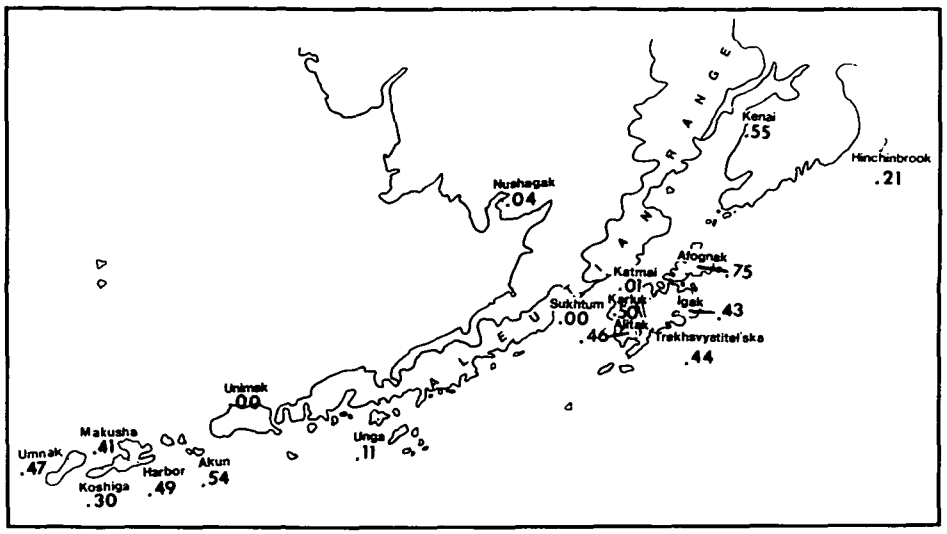


FIGURE 1 The distribution and frequency of the *B* gene in fox populations of Russian America in 1824.

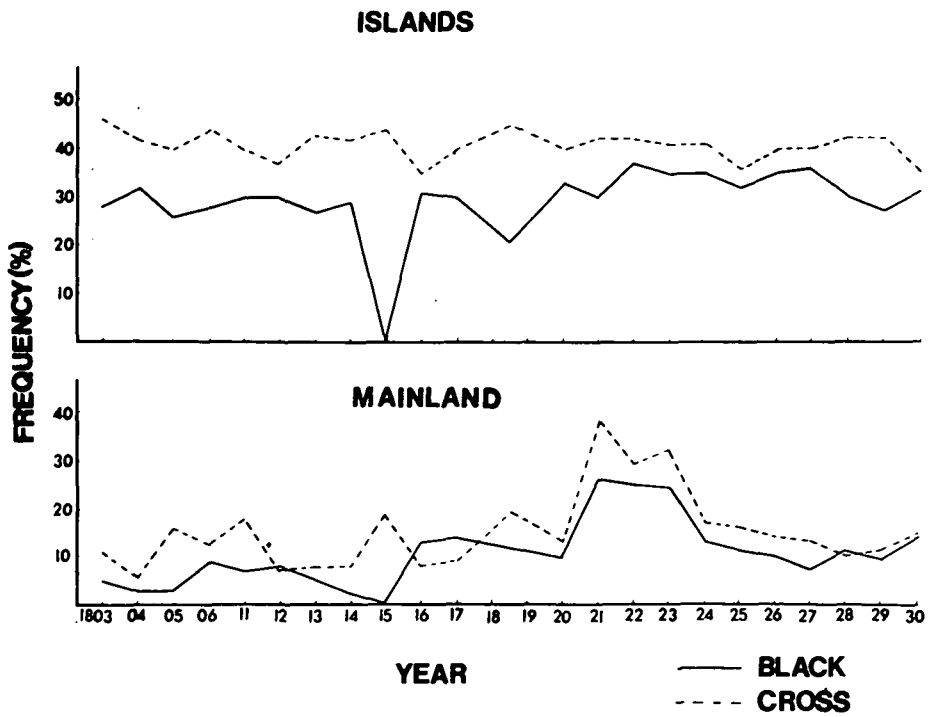
specific way of transporting migrants. A more coherent and general explanation is offered. It rests on the fact that the same distribution pattern of the *B* allele is observed over vast territories in Russian America and the Far East. While negligibly small on the mainland (0.05), the *B* allele frequency ranges about 0.50 in the islands. This tendency is widespread and has persisted over a long span of time. In evolutionary terms, the differences in gene frequencies may well be due to the different selection forces on the mainland and islands.

The information gathered by Khlebnikov encompasses a period of 1803–1830 enabling a tracing of the time course of changes in gene frequencies. He considered his data for mainland and island populations without assigning them to local population groups and, as a result, phenotypic distributions in such samples deviate from Hardy-Weinberg equilibrium. Nevertheless, the general time course of changes in phenotypic frequencies gives an idea of the direction and intensity of natural selection for the genes in question.

As regards the frequency of the Canadian silver-black gene, it has been shown to decrease smoothly from year to year, 1834–1933[7] and 1916–1941[3]. No such decrease is observed for foxes of Russian America throughout the years 1803–1830 (Figure 2). In both populations—on the mainland and islands—phenotype frequencies remained unchanged. A transient, almost twofold rise in the frequencies of black and cross foxes in the mainland sample of 1821–1923 is the possible result of increase in the supply of pelts by the Kenai station. There are no black foxes in the 1815 sample, presumably because it is too small.

The data on the time course of changes in the frequencies of the phenotypic classes do not suggest any differences in their selective value either on the mainland, or on the islands. Quite obviously, far reaching inferences concerning variations in gene frequencies cannot be made from an analysis of a short period of 30 years. The *B* gene frequency has, nevertheless, remained remarkably stable from 1697 to 1930 on the Kamchatka Peninsula. Comparisons of the genetic profiles of Alaskan fox populations, as described by Khlebnikov, with the latest data would perhaps disclose changes in the gene pool that has occurred over 150–180 years.

FIGURE 2 Time course of changes in the phenotype frequencies of island and mainland fox populations of Russian America in 1803–1830. (These data were derived from Khlebnikov[12] (p. 26–30).



Mainland vs. Island Populations

With these considerations in mind, the differences in the genetic profiles between the mainland and island populations may be tentatively accounted for as follows: 1) the distribution of gene frequencies observed is the result of natural selection in favor of black foxes on the islands. On the mainland, natural selection disfavors this color phase. 2) The high level of polymorphism in the islands is maintained by regular changes in selection vectors. These changes occur because ecological conditions on the islands are less stable than on the mainland.

These explanations are not mutually exclusive, and neither one is more convincing than the other. What is certain is

that they both abut on the question: what makes a particular phenotype selectively valuable? Selective values seems to be based much more on differences due to multiple effects than on the protective role of coat color. In fact, melanics (mice, rats, foxes) are generally more resistant to stressing agents than their standard colored counterparts[9-11]. For this reason, darkened coloration of cats is of adaptive value in an urban setting, and, accordingly, the frequency of the *a* gene (non-agouti) producing black color is higher in this setting than in rural areas[17].

In 1755, Krasheninnikov, a pioneer of Kamchatka, unawaredly described one of the pleiotropic effects of the *B* gene. He noted[13] the belief not only of aborigenes, but also of Russian hunters, that the more prized foxes (black and sivodushkas) are more elusive and are unsurpassed in their cunning evasiveness. To illustrate, he recounted the experience of a skillful hunter, a local Cossack who tracked a vixen for two winters in the tundra; but in no way did he contrive to lure her into a trap, or to outwit her. This behavioral trait surely conferred advantage under inexorable selection.

Since men's stressing interference into wildlife was stronger in the more densely populated islands of Russian America, so were the consequences.

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