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GENERAL BIOLOGY

The Results of Sable (*Martes zibellina*) Reintroduction Demonstrate the Founder Effect

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Abstract—The relative abundance of intrapopulation groups with different parameters of skull size, coat color, and expression of an epigenetic cranial trait was compared in autochthonous, reintroduced, and donor populations of sable. Recovery of the species resources and broad variability of the phenotypic trait complex in the newly fomned populations were observed. A large proportion of the animals had the phenotype that included large size, dark coat color, and pronounced expression of a specific phene trait (foramen in the condylar fossa) and was not characteristic of the neighboring autochthonous populations. It is reasonable to attribute the presence of individuals with an unusual morphology in the newly formed populations of animals to a manifestation of the founder principle, because the effect of this principle was promoted by spatial isolation of the primary foci of translocated animals.

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The founder principle term and concept were proposed by Mayr [1] to explain the causes of the emergence of unusual forms (morphs) of organisms upon the expansion of species to new territories. The founder principle is considered one of the evolution factors in the modern evolution theory, a law that states that the founder of a new isolated community or insular population carries only a small part of genetic information present in the population or species of origin of the founder individual. As a result, a novel phenotypic appearance of the new population, which is different from that of the major population, is formed. The results of some studies in natural and experimental systems disprove this principle [2], whereas other studies confirm it [3, 4].

The effect discussed can be related to the bottleneck phenomenon, which affects a group of individuals colonizing a new territory. Moreover, the founder principle cannot be implemented in the absence of isolation of the new population. The authors of [5] supposed that the phylogeny of such species as the cheetah *Acinonyx jubatus*, the snow sheep *Ovis nivicola*, and the chamois *Rupicapra rupicapra*, involved all these mechanisms. This is also true for the species subjected to introduction (translocation), an applied biotechnology approach intended for the preservation of valuable game animal resources exhausted by excessive hunting [6].

Does this principle hold true for reintroduction of animals? We addressed this issue using sable in Russia as an example. The results of this study are presented here.

Researchers became concerned about the dramatic decrease of sable population size in the mid-20th century. The species was fully eliminated from some regions of the country, and the decision to restore the resources by re-settling the animals from the remaining habitats (reintroduction) was made.

A number of populations of the species are believed [7, 8] to have emerged due to reintroduction into the unoccupied parts of the living range (Table 1). As reported in [7], the number of sables reintroduced into these areas from the five major capture areas in 1940–1959 was 3648, the main capture areas being the lower reaches of the Vitim River (1229), the Barguzin Ridge (797), the Chamar-Daban Ridge (1002), the upper Bureya River (569), and the Kamchatka Peninsula (51). Animals from two to three capture areas were resettled in most introduction areas. The origin of resettled animals in each of the reintroduction areas is shown in Table 1.

The condylobasal skull length was measured in adult sables in order to characterize the size of the animals. The numbers of "small" and "large" individuals were calculated for each group. The delimiting values (average value of this parameter from the author's craniometric database for the species, $n = 9999$) for the

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Table 1. Capture sites (data from [7]) for the sables translocated to reintroduction sites

Reintriduced populations	Founders (%)					Total (3648)*
	Vitim River (1229)*	Barguzin ridge (797)*	Chamar-Daban ridge (1002)*	Bureya River (569)*	Kamchatka peninsula (51)*	
Vakh River	57.8	21.1	21.1			531
Kazym River	52.1	19.0	29.0			511
Tomsk oblast	32.2	38.6	29.3			1141
Sym and Elogui Rivers		50.0	50.0			296
Tannu-Ola ridge			100.0			260
Kolyma River (upper reaches)				100.0		361
Kolyma River (middle reaches)	52.7			38.0	9.3	548

* The total number of animals captured for reintroduction is shown in parentheses.

Table 2. Frequency of occurrence (%) of different phenotypes in founder, reintroduced, and autochthonous sable populations

Areas	Animal sex	Founders	Reintroduced animals	Autochthonous
		% large		
Western Siberia	Males	***18.4*** (316)	64.7 (422)	***87.4*** (342)
	Females	***12.0*** (301)	59.5 (378)	***88.1*** (319)
Yenisei Siberia	Males	***13.6*** (220)	33.9 (183)	43.1 (195)
	Females	***11.3*** (221)	36.5 (104)	38.6 (171)
Far East	Males	***49.2*** (669)	69.8 (129)	80.2 (131)
	Females	47.1 (575)	54.4 (125)	***78.0*** (91)
		% individuals with the FFCI phene		
Western Siberia	Males	***50.0*** (460)	36.9 (442)	***20.1*** (810)
	Females	***69.4*** (422)	54.2 (395)	***37.7*** (779)
Yenisei Siberia	Males	53.2 (295)	53.4 (253)	47.9 (167)
	Females	*73.1* (312)	62.4 (178)	68.0 (169)
Far East	Males	*37.5* (733)	51.5 (130)	*40.0* (225)
	Females	***54.1*** (615)	72.8 (125)	*57.3* (199)
		% individuals with dark fur		
Western Siberia		***72.4*** (170 597)	51.0 (123 364)	***15.6*** (80 322)
Yenisei Siberia		***71.2*** (73 159)	54.7 (13 623)	***40.5*** (121 041)
Far East		77.8 (19 4601)	78.4 (31 685)	***57.2*** (23 761)

Significance level for the comparison to reintroduced population parameters: italicized at $p < 0.05$; bold italic at $p < 0.001$. The number of animals in the samples is given in parentheses.

size were 82.7 mm for males and 75.8 mm for females. The data on males and females were analyzed separately because of apparent sexual dimorphism. The data on the number of animals in each set investigated are presented in Table 2. The number of skulls analyzed was 4892, including 2607 skulls from males.

The frequency of occurrence was also studied for the opening in the condylar fossa (foramen in fossa condyloidei inferior, FFCI [9, 10]), a cranial epigenetic trait. The number of animals that had one (on the left or on the right) or two openings in the skull was counted for males and females separately in a combined set of 6709 animals (3515 ♂♂, 3194 ♀♀, Table 2).

The number of sable skins analyzed for coat color comparison was 832 153 (Table 2). Color classification of the skins was performed by fur experts of the state down-and-fur depots and procurement agencies in 1950–1992. The *All-Union Standard for Raw Sable Skins* OST NKZag-414 used in the classification divides all sable skins into seven color categories, similarly to the division for the American marten *Martes americana* [11]. Skins of the "extra dark," "dark," and

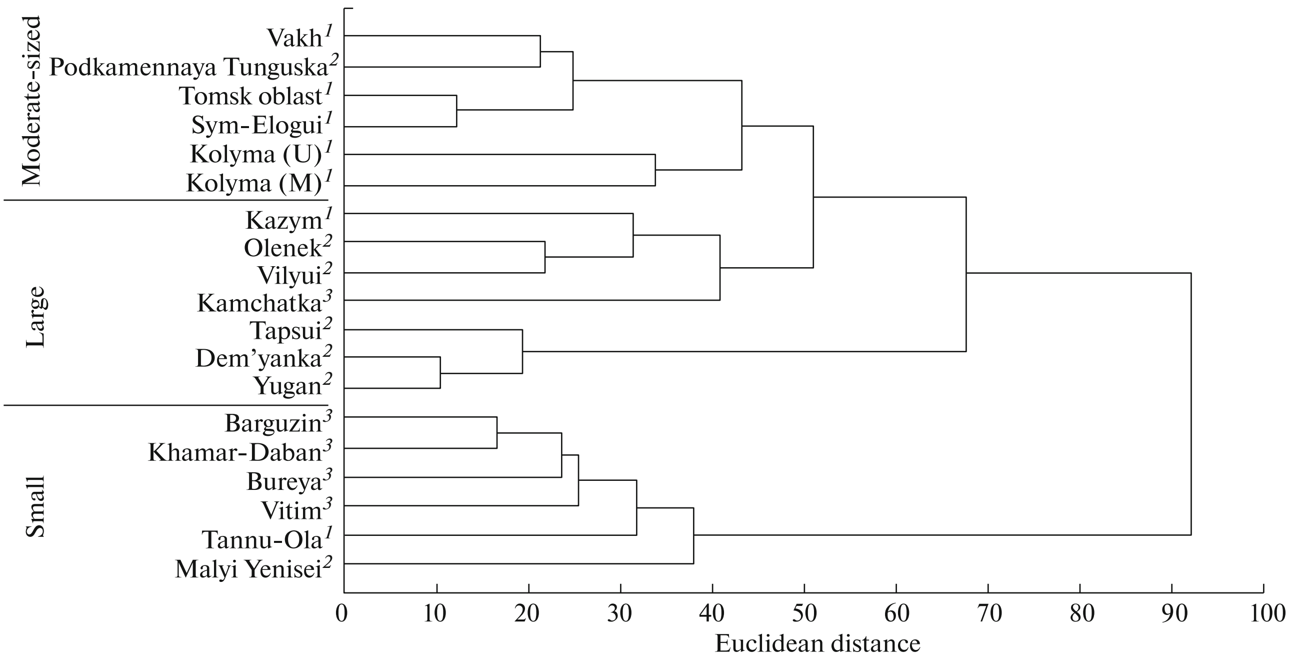

Fig. 1. A dendrogram of similarities and differences of the combined phenotypic properties according to UPGMA cluster analysis of the sable populations studied: *1*, introduced; *2*, autochthonous; *3*, founders.

"dark brown" categories were considered as "dark," and the "brown" and "light brown" ones were considered as "light."

All characteristics (Tables 1 and 2) were compared in three geographical macrogroups: the founders, the reintroduced animals, and the autochthones. The autochthonous populations of Western Siberia live along the Tapsui, Dem'yanka, and Yugan rivers, those of Yenisei Siberia, along the Podkamennaya Tunguska and Malyi Yenisei rivers, and those of the Far East, along the Olenek and Vilyui rivers.

As shown in Table 2, broad geographical variability of all traits is characteristic of all sable populations studied, and therefore multiple subspecies races can be identified, as described in [12]. Therefore, genetic pool mixing in the case of resettlement over hundreds or thousands of kilometers is not surprising. The major distinctive feature of relocation consisted in the preferential resettlement of sables into the unoccupied parts of the species range.

The morphological parameter values for the individuals from all sets studied were subjected to cluster analysis, and the results are shown in Fig. 1. We observed the following relationships. Almost all reintroduced animals (descendants of small founders) were classified as moderate-sized, and animals from the Tannu-Ola ridge were classified as small, but the Kazym sables attained almost the same size as the autochthonous animals of the Ob region. Furthermore, all animals inherited the dark pelage from the founders that (with the exception of the Kamchatka founders) were logically included into a cluster of sables with a small size, dark pelage, and high frequency of the FFCI phene. The cluster of large sables was also logically composed by autochthonous groups of animals with a light fur color and a low FFCI frequency.

Thus, comparison of morphological traits of sables from the populations formed due to reintroduction to the parameters of animals from founder and autochthonous populations revealed the presence of animals with phenotypes not characteristic of the area in the newly formed communities. For example, 15–37% of the animals in the new Western Siberian populations, where the local sables are large, with a light fur and low expression of the FFCI phene, had an unusual phenotype with a large size, dark pelage, and moderate frequency of the phene (Table 2). The proportion of animals with this phenotype in Yenisei Siberia ranged from 5 to 14%. Sables with a phenotype different from the aboriginal one also inhabit the Kolyma River basin (10–24% of the animals are large and characterized by a dark fur color and strong expression of the phene investigated).

Thus, we can conclude that the phenomenon observed, namely, the presence of unusual morphology in newly formed animal populations, can be attributed to the manifestation of the founder principle, which was promoted by the spatial isolation of the primary foci of resettled sables. The results of sable reintroduction in part of the regions within the species range demonstrate that the founder principle holds true and forms the prerequisites for microevolutionary transformations in the new populations, evolutionary stability of the species, and an increase of intraspecies diversity.

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