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To the Memory of famous beaver investigators
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BIOLOGICAL AND GENETIC PECULIARITIES OF CROSS-COMPOSED AND ABORIGINAL BEAVER POPULATIONS IN RUSSIA

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Abstract. A comparative review of the existing data on biological, genetic peculiarities of five autochthonous and five created by translocations beaver populations was carried out. It revealed that cross-composed populations were characterized by an evidently higher level of protein polymorphism, heterozygosity and by DNA variability. The reproduction rate of these populations is usually greater and they are more resistant to hunting pressure. In aboriginal populations and also in the areas where beavers have repeatedly passed through a genetic bottleneck more dental anomalies and other negative phenomena were observed. To conclude, highly productive cross-composed populations are of great value for game husbandry while aboriginal forms – the product of natural selection – are important components of recent biodiversity.
Key words: beavers, *Castor* sp., bottleneck effect, reproduction, game management, conservation

Introduction

70 years ago due to overhunting beaver (*Castor fiber*) was an endangered or even extinct species not only in Russia but in many countries of Europe, Asia and North America as well. The threat of losing this animal which is one of the most valuable game subjects made us take extraordinary measures. The global move towards its preservation has been successfully carried out in the Old and New Worlds. It was sufficiently well documented and described in many monographs. However, serious attention was not paid to the genetic estimate of the effect produced by large-scale translocations as well as the results of long-term passive conservation of local populations of this animal. This paper aims at making an evaluation of the above phenomena.

Some results of beaver translocations

According to the latest calculations (Safonov 1995), during the recent 70 years over 15,000 Eurasian (*Castor fiber*) and over 800 Canadian beavers (*Castor canadensis*) were translocated on the territory of the former Soviet Union. In recent years such work has been reduced to the minimum. The last translocation of Eurasian beavers in Russia took place in 2001 in Yakutia. The initial stage of this preservation action focused on the main stock of Belarusian and Voronezh beavers. However, later on it expanded to embrace daughter and/or cross-composed populations of beaver. At present the number of beavers is estimated (in 1,000s individuals) at 232.5 – in Russia, 23.7 – in Belarus, 6.0 – in the Ukraine, 2.2 – in Kazakhstan. In 63 out of 89 areas of Russia (republics, regions and autonomous areas) beaver is the subject of trapping and hunting. In some of them it is even the main furbearing species (Safonov & Saveljev 2001). In Kaliningrad region for some years all-year-round beaver harvesting has been already permitted. During the hunting season of 2001/2002 a Russian trapper earned up to 640 rubles per fell he sold, that is equivalent to USD 22.0. Some firms bought dried castoreum at a price of 1 ruble per gram, that made up almost half of the fell cost.
Sometimes in the process of beaver translocation animals of different origin were released into the same river basin. As a result, cross-composed populations formed which were found to have certain biological peculiarities. One of such populations is reported in

Kirov region. It numbers over 20,000 individuals (according to the official data of the Regional Hunting Department – 25,643 individuals in 2001). The average population density on the whole territory of the region makes up 18 individuals per 100 km^2. The beaver reproduction rate in Kirov as a vast number of facts has shown (Safonov 1971; Grevtsev 1979) is noticeably higher than that in all neighbouring regions and even in southerner latitudes where climatic conditions are more favourable. It amounts to 3.4 juveniles per female (Table 1). Such high reproductive potential has enabled the population to bear the heavy hunting pressure for 40 years already.

The reproduction rate increase was observed not only in cross-composed, but also in 'daughter' populations even in regions with severe natural conditions as compared with the initial ones. For example, the reproduction rate of Belarusian beavers, which were translocated from the Berezina River basin to the basins of the Desna and the Irtysh Rivers, increased by 7% in new habitats (Stavrovski 1986).

Thus, from the viewpoint of management, the results of the beaver conservation programme initiated 70 years ago may be evaluated as highly successful. The following indices prove that the historical area has been nearly restored, highly productive populations have been created, beaver fur being of great importance for fur industry of the country.

Problems of aboriginal populations

The situation of autochthonous forms of beaver is quite opposite. All of them are described as subspecies of Eurasian beaver *Castor fiber*: *belorussicus*, *orientoeuropaeus*, *tuvinicus*, *pohlei*, *birulai*. Each of these forms is beset with problems of some kind.

The population of autochthonous Tuva beavers (*C. f. tuvinicus*) on the Azas River did not outnumber 80 individuals during the last several decades. The possibilities of distribution extension to highlands by natural dispersion of beavers have been practically exhausted (Saveljev *et al*. 2000).

Other local population of beaver (*C. f. pohlei*) on the Konda River (the basin of the Ob River) also listed in the Red Data Book of the Russian Federation is in the state of long stagnation. Therefore even the most adherent supporters of wildlife conservation in Russia promoted the idea of artificial dispersal in West Siberia of animals that are successfully adapted to the south of the region but not the aboriginal ones (Shtilmark 1996). It is precisely these beavers successfully naturalized in the south of Tyumen region, that were introduced to Central Yakutia in summer 2001.

Although Siberian authochthonous forms – *tuvinicus* and *pohlei* were listed in the Red Data Book of the Russian Federation (2001), their status still causes anxiety. The pessimism of aboriginal beaver supporters and the optimism of those supporting acclimatization increase when comparing those forms with cross-composed populations thriving even under the pressure of intensive hunting.

Let us study the problem from the viewpoint of genetics and population biology, taking the so-called 'bottleneck' of the low population number into account. The present-day level of biological knowledge makes it possible to say rather definitely what significant effect genetic polymorphism produces on the reproduction rate and general welfare of populations (Gershenzon 1974; Altukhov 1995).

Lately in Russia as well as in a number of other countries studies have been carried out to estimate the level of genetic variability in populations that have different status and different genealogy. Our investigations

Table 1. The average reproduction rate of Eurasian beavers in populations of different origin.

Populations/ river basins	Origin	n	Reproduction rate	References
Konda	Aboriginal	26	1.4	Vasin 2001
Azas	Aboriginal	5	1.7	Saveljev *et al*. 1999
Elbe	Aboriginal	22	1.9	Nolet *et al*. 1994
Voronezh	Aboriginal (?)	24	2.8	Dezhkin 1961
Berezina	Aboriginal	68	2.9	Stavrovski 1986
Biesbos	Daughter (of Elbe)	14	2.5	Nolet *et al*. 1994
Oka	Daughter (of Voronezh)	125	2.9	Kudryashov 1975
Desna	Daughter (of Berezina)	28	3.0	Stavrovski 1986
Irtysh	Daughter (of Berezina)	20	3.0	Stavrovski 1986
Vyatka	Cross-composed (Voronezh + Berezina)	102	3.4	Grevtsev 1979, Safonov 1971

(Milishnikov *et al*. 1997) have shown that the cross-composed populations *C. fiber* in Kirov region have an unusually high level of protein polymorphism – 0.38; number of loci n = 45. The level of polymorphism turned out to be significantly higher not only than that in aboriginal beavers of the Berezina and Voronezh River basins, but it also exceeded the average level of polymorphism in small mammals – 0.156 (Tiedemann *et al*. 1996). Genome supervariability of Kirov beavers was confirmed by DNA fingerprinting analysis made by Swedish biologists. The level of DNA variability as well as that of the biochemical one in the Vyatka population was several times higher than that in Scandinavian beavers. For instance, in the cross-composed Kirov population it fluctuated within the range of 47.2–55.3%, while in Swedish beavers it was only within the range of 10.8–23.6%, and in Norwegian rodents it was even lower: it varied from 6.5 to 20.4% (Ellegren *et al*. 1993).

The above data seem to suggest that daughter (non-cross-composed) populations formed by artificial translocation and thus, passing through the stage of bottleneck lose a considerable level of genetic variability and do not restore it even during the rapid expansion of the population under favourable conditions on the sites of introduction.

That statement was corroborated by electrophoretic studies of Canadian beavers in South Carolina (Hope *et al*. 1984) and the estimate results of the major histocompatibility complex (MHC) variability level in Swedish beavers of Norwegian origin (Ellegren *et al*. 1993). Even more surprising results have been recently obtained in Lithuania. As it is known beaver resources in this country are the result of cross-composition of Voronezh and Belarusian beavers. And in those rodents the level of protein polymorphism turned out to be even higher than in the cross-composed Kirov beavers. So, according to the data (Paulauskas & Ulevičius 2000), all of the examined 12 loci in Lithuanian beaver populations (n = 24) were polymorphous (p = 1.00). That is the rarest phenomenon in wild animal genetics. The number of alleles in each of those loci varied from two to six. The level of heterozygosity in Lithuanian beavers was unusually high: it ranged from 0.561 to 0.668. The authors logically assume that both the present-day genetic status and high rate of population increase have been predetermined by the population formation history.

On the other hand, the level of genetic erosion is especially high in those beaver populations which are repeatedly passing through (due to certain historical conditions) the small-size stage of small quantity (the so-called 'bottleneck'). As our studies showed (Saveljev 1989) Canadian beavers have experienced the genetic bottleneck at least four times since 1937 when they were introduced from the state of New York into Finland. Then in the mid-1940s they spread to north-western regions of Russia and from that area they were reintroduced once more, this time into the regions of the Far East. The population that formed near Khabarovsk shows outstanding abilities to use the territory: not only did the animals entirely occupy the Obor River basin, but they also crossed the watershed and were observed on some tributaries of the Ussuri River. However, unusually high occurrence of different dental abnormalities was found in that population of acclimatized animals. Here 30% of individuals had carious teeth and signs of parodontosis. Oligodontia was typical of 15% of animals, and 7% of them had extra teeth (Fig. 1; Saveljev 2001).

High occurrence of tooth anomalies was also found in the population of autochthonous beavers (*C. f. albicus*) in East Germany. There 8.7% of individuals, i.e. almost one out of every ten Elbe beavers, had a pathology of dental system (Piechocki 1977). Undoubtedly, this is the outcome of the bottleneck, which the population experienced some decades ago.

It is absolutely clear that for rodents whose feeding habits are the same as those of beaver dental problems turn to be the greatest negative factor hindering the population welfare.

And here are some comments about one more peculiarity that is, undoubtedly, genetically determined. East Europe and Siberia are inhabited by beavers of two colour morphs – brown and black. There are sufficient grounds to assume that beavers-melanists appeared as a result of direct selection according to fur colour that was started in Poland in the 13th century (Wdowinscy & Wdowinscy 1981). In different regions of the Soviet Union and Schwerin lakes in Germany there were attempts to create monomorphic beaver populations. At present one of such populations where 100% of beavers are melanists with the highest-quality fur inhabit the upper reaches of the Pechora River.

We have studied the population 37.5% of which are made up by black individuals (Milishnikov *et al*. 1997; Milishnikov & Saveljev 2001). The analysis of 52 allozyme loci showed that there is a relationship between the fur colour and genetic parameters of the population. The group of black beavers had a slightly lower level of protein polymorphism and heterozygosity than brown individuals (p = 0.33 as against 0.48; H_o = 0.069 as against 0.087). Thus, lower-level genetic variability is typical of black beavers with the fur of great utilitarian value. Beaver resource management programmes should certainly take this peculiarity into account.

Man has restored beaver resources owing to considerable physical efforts and financial expenses that mass

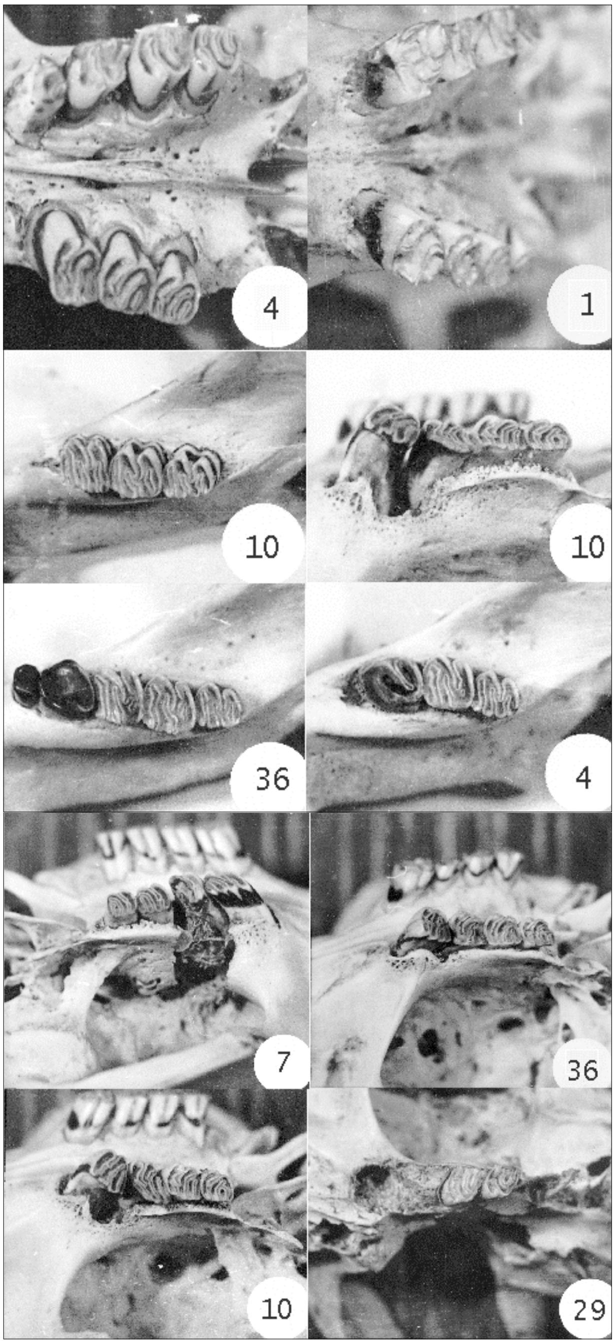

Figure 1. Dental abnormalities of the Canadian beaver population which has passed through a bottleneck four times (Saveljev 2001). Figures indicate the cranium collection number.

artificial dispersal of these rodents has entailed. At present about 90% of these resources in Russia are the offspring of Belarusian and Voronezh animals and their cross-composed representatives in various combinations. As before autochthonous forms have the status of endangered animals.

For comparison, in North America the first half of the 20th century was the period of active taxonomical description of beaver diversity. Three species and 24 subspecies of North American beaver were described (Cahalane 1947; Hall & Kelson 1959). However, later on unlimited harvesting caused a dramatic decline in the number of beavers, subsequently followed by the translocation boom. Since that time American zoologists practically have not shown any interest in that branch of investigations. Even publications on geographical variability are scarce (e.g., on cranium sizes). This study was carried out for the purpose of verifying ecological-geographical rules, but not for that of taxonomical revision of the species (Dillman & Barnett 1985).

Parallels

Beaver is one of a few species though not the only one, which have suffered a profound effect of human activities. Our forefathers were also users of nature and had similar 'interrelations', for example, with Pheasant (*Phasianus colchicus*). In the 13th century on the territory of Europe as a result of hybridization of various Asian and Caucasian taxonomic forms the so-called 'hunting pheasant' was bred. It was characterized by better flying abilities (an important quality for sport hunting) and a greater tendency towards synanthropization (Eggeling 1999). Of game ungulates it was red deer (*Cervus elaphus*) that was most strongly affected by human activities. At present red deer is one of the most important and prestigious hunting subjects in Europe. However, it seems obvious that at present game biologists of the Old World are concerned about the problem of the increasing area fragmentation and the decreasing trophy quality of animals, but not about the problem of conservation of the taxonomic status of certain subspecies. Zoological problems of the species receive least attention in New Zealand where the offspring of Scottish deer that are naturalized and thriving in the new environment have actually become subjects of intensive animal husbandry. Priorities given to reaching high productivity and good genetic quality of the livestock in Germany are rather clearly expressed by scientists (Wagenknecht 2000) and by hunters (Menzel 1998).

Conclusions

The most heterosical beaver populations that formed during the recent decades on the territories of Russia, Lithuania, Poland, Bavaria as well as many other regions of the Old World show (to a greater extent rather occasionally) high ability of these rodents to use territories and resist hunting pressure. Higher rate of reproduction and greater viability are characteristic of them. Sheer absence of equivalence between the products of natural and artificial selection is often the cause of the fact that users of natural resources show preference to the forms more productive and valuable from the utilitarian point of view.

From the biodiversity conservation standpoint aboriginal forms are of no less value. Not numerous populations of autochthonous beavers are the natural process 'products' that represent the specimens of good adaptability to natural conditions. Such relicts may be significant elements of the 'reconstruction' of the natural history of the genus *Castor*. That fact alone is significant enough to take maximum care of them.

High-rate reproduction the basis of which is the effect of heterosis, and inbreeding depression are two alternative biological processes in organism growth. All symptoms of inbreeding depression can and are to be eliminated by recent methods of conservation biology both in protected animal populations, and in the case of game resource management.

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Rusijos hibridinių vietinės kilmės bebrų populiacijų biologinės ir genetinės ypatybės

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Santrauka

Buvo atlikta lyginamoji esamų duomenų analizė apie penkių vietinės kilmės ir penkių reaklimatizuotos (hibridinių) bebrų populiacijų biologines bei genetines ypatybes. Hibridinėms populiacijoms yra būdingas žymiai aukštesnis baltymų polimorfizmo, heterozigotiškumo lygis bei didesnis DNR kintamumas. Šių populiacijų vislumas yra paprastai didesnis, todėl medžioklės poveikis neturi didelės įtakos jų gausumo dinamikai. Aborigeninių bebrų populiacijose ir tose, kur bebrų gausumas buvo sumažėjęs iki kritinės ribos, užregistruota daugiau dantų bei kitų morfologinių anomalijų. Vislios hibridinės bebrų populiacijos yra labai vertingos šių kailinių žvėrelių eksploatacijos požiūriu. Tuo tarpu aborigeninės bebrų formos, kaip natūralios selekcijos rezultatas, yra svarbus bioįvairovės komponentas.

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