On morphology and genetics of a successfully restored beaver population in Lithuania

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Abstract: At least six centres of spread of reintroduced or naturally immigrated animals have influenced the formation of the present beaver (*Castor fiber*) population in Lithuania. Phenetic (non-metrics of skull) and genetic (allozyme electrophoresis) analyses show that beaver subpopulations of different origin have preserved their specificity even in conditions of dense population, 30-40 years since the first releases and arrivals. This specificity might be the result of the founder effect in small geographically and temporally isolated groups of reintroduced beavers. Conversely, subpopulations from the supposed zone of intensive hybridisation were found to be very phenetically similar. Metric parameters of the skull varied slightly among subpopulations, showing the higher metric differentiation between reintroduced beavers and natural immigrants. However, beaver skulls from Lithuania were found to be significantly larger than those from the basic maternal population in the Gomel region (Belarus) and of similar size when compared with the skulls from the Voronezh population (Russia). Our investigations show the complicated morphological and genetic structure of a hybrid beaver population and its considerable morphological changes in comparison with the maternal populations.

Keywords: Castor fiber, hybrid population, non-metric parameters, metric parameters, allozymes, morphological relationship, biochemical relationship, morphological differentiation, Lithuania.

Introduction

During the last centuries the European beaver (*Castor fiber*) has survived a drastic decline in population numbers which has gone as far as extinction in many regions of the continent. Small and isolated relict populations became the only materials available to restore the former species range. The most intensive work on beaver reintroduction was carried out in the middle of the 20th century (Lavrov 1981, Macdonald et al. 1995, Halley & Rosell 2002).

Nowadays the process of restoration of the European beaver populations in a number of European countries still continues. Reintroduced beavers have usually extended their range even to neighbouring countries (e.g. Nitsche & Pachinger 2000), thus showing the undoubted success of reintroduction as well as the high vitality of reintroduced populations. The general development pattern of many reintroduced beaver populations is relatively rapid increase in both the population number and range of expansion (e.g. Hartman 1994, Balodis 1990).

The question is why the reintroduced beaver populations are so viable, even when exploited relatively heavily. In this context we should remember that many aboriginal beaver populations were very vulnerable and became extinct in former centuries. On the other hand, it is important to know what the prospects for the restored populations are. Is vitality or welfare of a population reflected on the morphological and genetic levels? Comparative investigations show distinct morphological differences between newly restored mixed and autochthonous but small beaver populations (Saveljev & Milishnikov 2002). Also, some daughter beaver populations demonstrate significant morpho-physiological changes when reintroduced into different ecological conditions compared with those of the maternal populations (Solovjov 1991).

The beaver population in Lithuania is one of the populations that was very successfully restored during the second half of the 20th century. It shows patterns of intensive development such as rapid expansion throughout the country, fast increasing in population number, high current densities in environments with very different habitat structures (Ulevičius 1997, Ulevičius 1999, Ulevičius 2001). A brief history of this population could be described as follows: start of formation of the population in the 1940s, rapid expansion and colonisation throughout the country over approximately 40 years (13-14 generations), high current population numbers despite comparatively high exploitation since the 1970s.

We started by investigating non-metrical characteristics of the skulls of Lithuanian beavers in the context of the origin of different local populations usually inhabiting separate river basins (Ulevičius 1992, Ulevičius 1993, Ulevičius 1994, Ulevičius 1997). Later results of morphological investigations were tested using biochemical markers (Paulauskas & Ulevičius 2001). Recent metrical investigations on beaver skulls were carried out with respect to both the differentiation of a restored population and its relationship with the maternal populations. The aim of the present publication is to summarise the results obtained by three different methods within the context of origin and morphological and genetic differentiation of a hybrid population.

Material and methods

Lithuania is situated on the southeast coast of the Baltic Sea (21°00'–27°00' E and 54°00'–56°30' N). The total area is 65,200 km^2. The entire territory is covered by river basins of the Baltic Sea tributaries. The mean density of the hydrographical network is nearly 1 km/km^2. There are about 3,000 lakes in Lithuania. Mean density of human population is 52.4 inhabitants/km^2. The course of restoration of the beaver population was reconstructed by studying the archival and unpublished documents as well as local publications and personal communications. Special attention was paid to the year when beavers appeared in a certain district for the first time.

The autochthonous beavers in Lithuania became probably extinct somewhere in the 1920s-1930s (Mickus 1988). In the 1940s, beavers

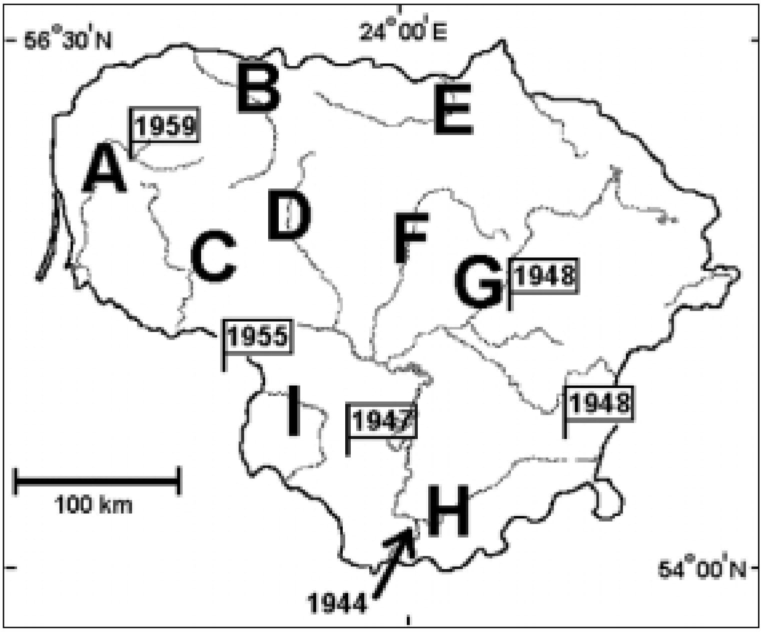

Figure 1. Location and year of beaver reintroductions in Lithuania (designated by flags), and location of samples (designated by capital letters, as in table 1). The black arrow designates spread of natural immigrants from Belarus, the upper reaches of the Neman (Nemunas) river basin.

appeared again in the country as a result of natural immigration and later as a consequence of intensive reintroduction. The genetic pool of the present beaver population in Lithuania has at least potentially been influenced by genetic material of a very different origin. Most reintroduced beavers originated from the Dnepr basin (Belarus). Also, beavers from Voronezh (Russia) may have had a significant genetic influence on some local populations in the southern part (possible gene immigration from Poland) as well as in northern Lithuania (possible gene immigration from Latvia). Phased release of relatively small groups of animals was the characteristic pattern of the reintroduction process. Thus, the genetic structure of such groups was rather strongly influenced by the founder effect, and possibly there were significant genetic differences between groups of animals even from the same maternal population but released at different times.

At least five geographically and temporally isolated reintroduction centres and one centre of natural immigration have influenced the formation of the current beaver population in Lithuania (figure 1). Beaver expansion was very quick and by the end of 1960s beavers were distributed throughout the country. This success was usually explained by favourable ecological conditions (Mickus 1988).

Morphological studies (non-metric and metric parameters) were based on a beaver skull collection sampled in 1986-1988, i.e. when large numbers of beavers were already inhabiting the entire country. Skulls were gathered from hunters during the hunting seasons. Hunters were asked to indicate detailed locality as well as sex and skin colour of a hunted beaver. After rough cleaning, the skulls were boiled for approximately two hours for final cleaning.

For non-metric analysis, 463 beaver skulls from nine local beaver populations were used (figure 1, table 1). These local populations inhabit different river basins: catchment areas of the 2-3 order tributaries of the Baltic Sea. The non-metrical (phenotypic) relationship was studied by analysing the frequencies of 63 variants (phens) of 19 non-metric traits (figure 2, table 2). Primarily, 40 non-metric traits of beaver skull were distinguished. Of them, twelve were rejected as being dependent on age and sex. Nine traits did not work (no significant differences among samples) at this level of intraspecific structural differentiation (Ulevičius 1993). Non-metrical distances were evaluated using the population similarity/dissimilarity measure for polymorphic characters (Zhivotovsky 1979). This method is based on estimating both the similarity index (*r*) and the identity criterion (*I*) (see Appendix).

For metrical analysis, a total of 103 beaver skulls were taken from five local populations of different origin (figure 1, table 1). Skulls with a closed basal foramen of premolar and molar teeth

Table 1. Samples (number of individuals) of beaver skulls for non-metrical and metrical analyses (sampled in 1986-1988) and liver for biochemical analysis (sampled in 1999-2002) from different river basins of Lithuania.

Sample code*	River basin	Skulls studied non-metrically	Skulls studied metrically	Liver studied biochemically
A	Minija	61	34	15
B	Venta	44	–	–
C	Jūra	79	–	–
D	Dubysa	52	16	2
E	Mūša	35	–	–
F	Nevėžis	48	–	–
G	Šventoji	60	23	35
H	Merkys	32	13	10
I	Šešupė	52	17	16
Total		463	103	78

* As in figure 1.

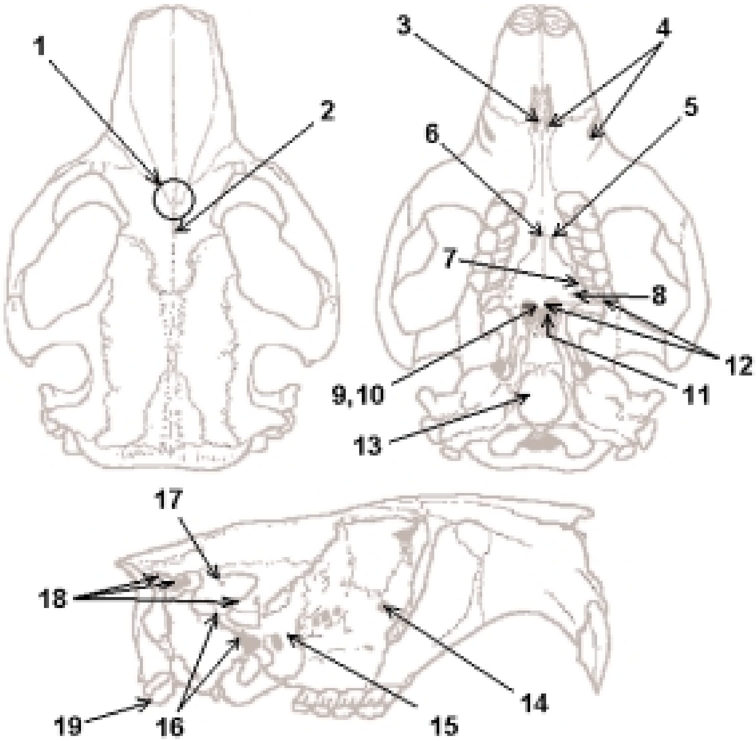

Figure 2. Location of non-metric parameters on beaver skull. Numeration as in table 2.

were analysed. In European beavers the basal foramen usually closes at four years of age (Safonov 1966). Thus, skulls of adult beavers (four years and older; 4+) were measured. For comparison with maternal populations, already published results of metrical investigations were taken from a monograph (Lavrov 1981): 1. Maternal population from Belarus (Sozh, Berezina), *n*=18, adultus. 2. Maternal population from Voronezh, *n*=52, senex (nine years old and older; 9+). 3. Maternal population from Voronezh, *n*=84, adultus (3-8 year old; 3+). Fifteen metrical characters of beaver cranium described by Lavrov (1981) were used for this study (figure 3, table 3). The accuracy of the measurements is within 0.1 mm. The significance of differences between two means in two-sample comparisons for every metrical parameter was evaluated using a *t*-test.

In four river basins containing subpopulations of different origin, livers from hunted beavers (a total of 78 individuals) were sampled for the biochemical (genetic) investigation in 1999-2002 (figure 1, table 1). After each trapping, livers were frozen at -20 ºC until preparation. Liver tissue homogenate was used for the electrophoresis of allozymes. For detailed descriptions see Paulauskas & Ulevičius 2001. The biochemical (genetic) relationship between samples was evaluated using 15 loci of four enzyme systems: malate dehydrogenase, malic enzyme, glucose-6-phosphate dehydrogenase and esterase, and two loci of non-enzymatic proteins. According to Rogers (1972), genetic distances express the biochemical differentiation among subpopulations.

Results and discussion

Phenetic and biochemical (genetic) structure of the restored beaver population

On the basis of non-metric analysis of skull samples studied local beaver populations were

Table 2. Description of the non-metric parameters of beaver skull.

Number	Parameter	Number of alternative variants	Character of variability
1	Frontal part of nasal bones	5	Shape
2	Frontal suture	2	Presence/absence
3	Process of the maxillary bone between incisive foramens	4	Shape
4	Incisive foramens with respect to infraorbital foramens	3	Position
5	Major palatal foramens	2	Number
6	Palato-maxillar suture between the major palatal foramens	2	Configuration
7	M^3 with respect to palatine bone	2	Presence/absence of contact
8	Additional foramen to the hind maxillary foramen	4	Size and position
9	Choan spine	4	General shape
10	Apex of the choan spine	5	Shape
11	Spheno-palatal suture inside the choan cavity	2	Configuration
12	Choan spine with respect to alveolar process	3	Position
13	Fissure on occipital hole	2	Presence/absence
14	Spheno-palatal foramen	4	Size and position
15	Lateral wall of the pterygoid canal	2	Presence/absence
16	Fissura ptero-tympanicum with respect to spheno-squamosal suture	3	Position
17	Temporal foramen	8	Number
18	Auricular tube with respect to auricular and zygomatic processes	3	Position
19	Occipital condyle with respect to the jugular process	3	Position
Total		63	

classified into two groups. Each group (A, E, H, and I; see table 1) could be described as a phenetically specific subpopulation. Each of them originated from different centres of spread. Each sample from these subpopulations showed highly significant phenetic distance from the other samples when compared with a complex of non-metric parameters (table 5).

Samples from the second group (B, C, D, F, and G; see table 1) showed far less phenetic specificity when compared to each other. No significant phenetic distances were found when a complex of non-metric parameters was used among samples of the second group (except between F and G; table 5).

These findings suggest a hypothesis about the presence of a zone of intensive hybridisation of the expanded beaver populations in the centre of Lithuania (samples C, D and F). There were no releases of reintroduced beavers in this part of the country. Most likely, the expanded beaver populations here originated from at least three centres of spread: Kaliningrad region (1955), Kertuša (Šventoji basin) and Krempa (1948), and natural immigrants from southern Lithuania (1944) (figure 1, table 4). On the other hand, high phenetic specificity of subpopulations of different origin suggests strong influence of the founder effect in small groups of reintroduced beavers and the ability to preserve this specifi-

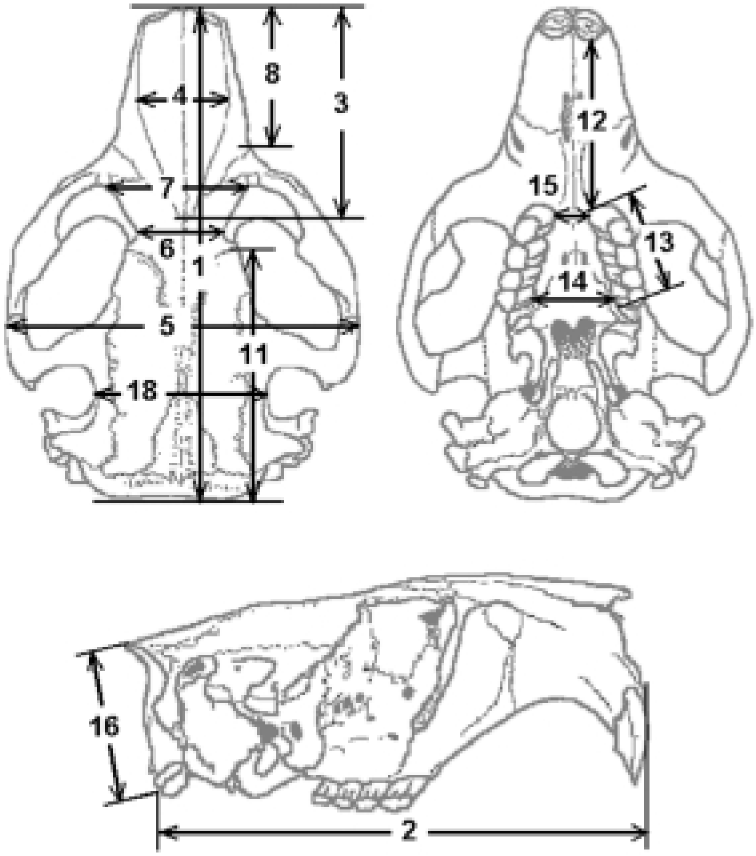

Figure 3. Metric parameters of beaver skull. Numeration of parameters as in table 3 by Lavrov 1981.

city even in conditions of high population density.

Analysis of beaver groups of different origin using biochemical markers displayed a principally similar relationship pattern among samples (figure 4a). The greatest biochemical distances were found between natural immigrants in the southern part of the country (Merkys basin (H)) and the most recently reintroduced subpopulation in north-western Lithuania (Minija basin (A)). However, biochemical clustering of samples was somewhat different than that using non-metric distances (figure 4b). Beavers from the Šventoji (G) and Minija (A) subpopulations are in one biochemical cluster whereas phenetically they differ significantly. Outstanding biochemical specificity of the Dubysa beavers (D) might be biased by the small and not representative sample (*n*=2). Observed inadequacy between non-metric and biochemical distances might be caused by a sampling bias, because the biochemical samples were much more restricted geographically than the craniological ones. Another possible explanation of this inadequacy could be the difference in sensitivity of biochemical and non-metric markers for finding differences among local populations. As was mentioned above, the non-metric parameters that showed no significant differences among samples were excluded from further analysis on the assumption that these parameters were not sensitive enough to expose differences among local populations. This was not done for the biochemical markers. Thus, it is possible that the last ones were less sensitive for detecting differences among local populations. The phenomenon of non-metric parameters of uneven scale has been widely discussed by representatives of popula-

Table 3. Metric parameters of beaver skull (used by Lavrov 1981).

Number	Number used by Lavrov 1981	Parameter	Notes
1	1	Total length of cranium	
2	2	Condylo-basal length	
3	3	Length of nasal bones	
4	4	Maximum width of nasal bones	
5	5	Maximum width of the cranium	Zygomatic width
6	6	Minimum interorbital width	
7	7	Frontal width	Between proximal points of the lacrimal bones
8	8	Length of the nasal part of the cranium	
9	11	Length of the hinder part of the cranium	From the postorbital process to extreme point of the occipital crest
10	12	Length of the upper diastema	
11	13	Alveolar length	Between the foremost point of the Pm alveolus and hinder point of the M^3 alveolus
12	14	Fore palatal width	Shortest distance between Pm alveolus
13	15	Hind palatal width	By centres of the M^3 teeth
14	16	Occipital height of the cranium	From the ground point of the bend between occipital condyles to upper point of the occipital crest
15	18	Temporal width of the cranium	

tion phenetics (see Jablokov & Larina 1985 for review).

Nevertheless, the question of which markers (morphological or biochemical) better reflect the real genetic relationship between the beaver subpopulations remains open. Our present investigation shows that the non-metric relationship fits better the data on origin of different subpopulations. In some other rodents it has been found that genetic variation, as measured by variation in allozymes, explains up to 50-80% of the heterogeneity among populations in levels of cranial (osteometric) variation (Soule & Zegers 1996). However, more detailed biochemical investigations are needed to be able to make well-founded conclusions concerning beavers.

Metric differentiation of skull samples

Metric comparison of the skull samples from five beaver subpopulations of Lithuania uncovered quite a regular and explainable (in context of origin) picture of the metric relationship among the subpopulations. Again, as in the case of non-metric and biochemical analyses, the greatest metric specificity was found in the Merkys basin subpopulation (sample H) originating from early natural immigrants from the upper reaches of the Nemunas basin. This sample differed significantly from other samples for four to six metric parameters of the skull (table 6). Other samples also showed significant metric differences. However, the number of parameters for which these differences were sig-

Table 4. Reintroduction and natural immigration of beavers in Lithuania and the neighbouring countries.

Origin	Year of reintroduction /immigration	Locality of release	Samples that could be most influenced	Number of released animals	Reference
Norway	1927	Irbe basin, Latvia	B	4	Balodis 1990
Natural immigration from a population in Grodno region, Belarus	Early 1940s	Merkys basin, Southern Lithuania	H	?	
Voronezh, Russia	1947	Žuvintas Strict Nature Reserve, Lithuania	I	8	
	1949	Osowiec, Northern Poland	I	6	Macdonald et al. 1995
	1952	Venta basin, Latvia	B	6	Balodis 1990
Dnepr basin, Sozh/ Berezina river system, Gomel region, Belarus	1948	Šventoji basin, Kertuša river, Lithuania	G	25	
	1948	Krempa river, Lithuania	?	15	
	1955	Šešupé- basin, Sovietsk district, Kaliningrad region, Russia	I	30	Beljakov et al. 1980
	1959	Minija basin, Lithuania	A	30	

nificant, appeared to be slightly or considerably less than in the case of sample H. No significant differences for any metric parameter were found between samples D and G. These two samples showed no significant phenetic differences either, suggesting a comparatively closer genetic relationship to each other than to the rest of the studied samples.

Unexpected results were obtained when skulls from Lithuanian beaver population were compared with skulls from two maternal populations: Dnepr basin (local basins of Sozh and Berezina) in Belarus, and from Voronezh region in Russia. From these populations were derived from almost all reintroduced beavers to Lithuania and the neighbouring countries (table 4). The biggest number of Lithuanian reintroduced beavers originated from the Dnepr basin (Belarus). Therefore, it is to be expected that all genetically determined characteristics of Lithuanian beavers would be closely related to those of Sozh and Berezina beavers. However, the skulls of Lithuanian beavers appeared to be significantly larger than the Belarussian ones, for 11 parameters out of 15. These differences were especially expressed in such general measurements as the total and condylo-basal length as well as maximum width of the cranium. For example, the average total length of the cranium of Lithuanian beavers exceeded the Belarussian one in 10 mm (table 7).

In terms of their size, the skulls of Lithuanian

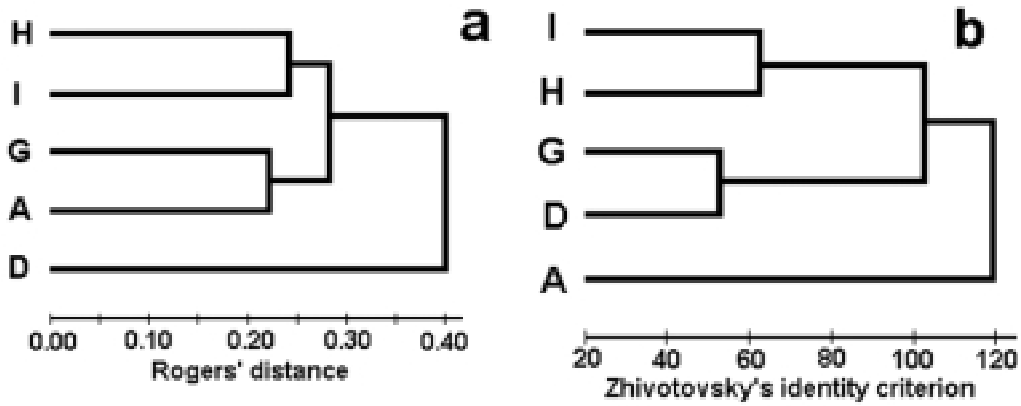

Figure 4. Genetic (biochemical) (a) and phenotypical (non-metric) (b) relationship among studied beaver subpopulations in Lithuania. Dendrograms were constructed using the UPGMA method. Codes of samples as in table 1 and figure 1.

beavers were found to be very close to beavers from Voronezh region. For seven parameters they were smaller than the Voronezh senex. However, when compared with the Voronezh adultus, the skulls of Lithuanian beavers were significantly larger for the majority of the parameters (table 7). Beavers from Voronezh are considered to be the largest among the other geographic forms of *Castor fiber* after beavers from the Elbe basin, Germany. On the contrary, beavers from Belarus were described as comparatively small among other geographical populations (Safonov 1966, Lavrov 1981).

Results of the metrical analysis could be somewhat biased by a possibly uneven age structure of the samples compared. Lavrov's adultus is defined as a 3-8 year-old (3+) (Lavrov 1981). Thus, a certain proportion of 3+ beavers could be present in the samples described by Lavrov (1981). As was mentioned before, we analysed only skulls with already closed basal foramen of premolar and molar teeth that is usually characteristic for the 4+ beavers (Safonov 1966). We also have not distinguished the senex age group (9+) (as Lavrov did) because in an intensively exploited beaver population such animals are expected to be rare. Anyway, big differences in average meanings of a number of parameters suggest that the age bias in this case is not of primary importance.

Why have Lithuanian beavers become so large? This cannot be explained by the founder effect because the majority of Lithuanian reintroduced beavers originated from the

Table 5. Non-metric distances (Zhivotovsky's identity criterion, I) for a complex of 19 non-metric parameters of skull among nine beaver subpopulations in Lithuania. Asterisks indicate the significance level: *= *P*<0.05, **= *P*<0.01, ***= *P*<0.001; ns = not significant.

Samples	A	B	C	D	E	F	G	H
B	125.5***							
C	107.0***	71.8**						
D	84.0***	52.2 ns	28.3 ns					
E	93.3***	75.3**	85.4***	65.9*				
F	105.7***	63.3*	77.8**	53.8 ns	73.9**			
G	91.3***	59.0 ns	76.3**	46.4 ns	72.5**	66.6*		
H	159.6***	109.6***	113.6***	90.4***	112.4***	83.2***	133.6***	
I	135.4***	110.0***	84.0***	62.2*	84.5***	82.0***	112.3***	65.5*

Table 6. Metric parameters of skull in which statistically significant differences were found among five beaver subpopulations in Lithuania. Figures indicate codes of metric parameters as in table 3 and figure 3 (numeration by Lavrov 1981); asterisks indicate the level of significance: *= P<0.05, **= P<0.01, ***= P<0.001.

Samples	D (*n*=16)	G (*n*=23)	H (*n*=13)	I (*n*=17)
A (*n*=34)	16*, 18***	18*	5***, 7*, 11*, 16**, 18***	14**, 15*, 16*, 18***
D		-	5**, 7**, 11**, 18**	14**, 15**
G			3**, 5**, 7*, 11**, 18***	2*, 3**, 6**, 14***, 15***
H				5**, 6**, 7*, 14*, 15***, 18***

Belarussian population(s) where "small beavers" live. The intersubpopulational hybridisation could result in a heterosis effect, at least in the supposed zone of intensive hybridisation. However, our findings at all three levels of analysis (non-metric, biochemical and metric) indicate certain (perhaps genetic) specificity of the studied subpopulations, suggesting that even in conditions of dense population the gene flow among the local populations could be minimal. Another cause of morphological changes in Lithuanian beavers could also be the exploitation effect. High levels of exploitation might promote higher levels of gene flow inside a subpopulation by incorporating the population reserve into the breeding process. In general, the mechanism could be described as follows: the more genotypes breed, the higher the proportion of the genetic pool of a subpopulation that can be realised in a separate individual. Mate replacement by immigrated beavers is a usual pattern in pair formation when one of partners is lost (Kudriashov 1975, Svendsen 1989). High loss of a beaver mate in a family can be expected when beavers are hunted using traps, because traps are usually set near the main lodge (personal communications with many Lithuanian hunters).We suggest that both processes (inter- and intra-subpopulational hybridisation) could bring about distinct morphological changes.

Another interpretation might be related to certain morpho-physiological adaptations of the reintroduced populations to their new environments. A reintroduced northern population living in conditions of eastern taiga and originating from Voronezh (zone of broadleaf forest) showed distinct morpho-physiological changes within approximately four decades after the first releases (Solovjov 1991). Significant morphological differentiation at a population level (among southern and northern populations) was found in the muskrat (*Ondatra zibethicus*) cranium originating from a genetically homogeneous group of animals (Vasil'ev et al. 1999). However, in the case of Lithuanian beavers this interpretation seems to be less acceptable because environmental conditions in daughter and maternal populations differ only slightly, thus the influence of genetic processes on morphological changes is expected to be more important.

Conclusions

The current beaver population in Lithuania has originated from at least three genetically different maternal populations. The majority of reintroduced beavers were from the Dnepr basin, Belarus. Five geographically and temporally isolated reintroduction centres, where the number of the released animals varies from 8 to 30, and one centre of natural immigrants have influenced the formation of the current beaver population in Lithuania.

Phenetic (non-metrics of skull) and genetic (allozyme e-phoresis) analyses showed that beaver subpopulations of different origin (from different maternal populations and different centres of spread) have preserved their specificity even in conditions of dense population. This specificity might be caused by the founder effect in small geographically and temporarily isolated groups of reintroduced beavers. On the contrary, subpopulations from the supposed zone of intensive hybridisation of reintroduced beavers and

Table 7. Differences in metric parameters of skull between Lithuanian beavers (*n*=103) and maternal populations from the Dnepr basin (Belarus) and Voronezh region (Russia). + = skulls of Lithuanian beavers that are larger; - = skulls of Lithuanian beavers that are smaller.

Parameter*	Dnepr basin (adultus, *n*=18), by Lavrov 1981		Voronezh region (senex, *n*=52), by Lavrov 1981		Voronezh region (adultus, *n*=84), by Lavrov 1981	
	Difference between two means (mm)	*P*	Difference between two means (mm)	*P*	Difference between two means (mm)	*P*
1	+10.0	0.0000	0	ns	+4.5	0.0000
2	+8.6	0.0000	-0.9	ns	+3.2	0.0000
3	+3.2	0.0000	-0.9	0.0259	+1.5	0.0000
4	+0.9	ns	+0.1	ns	+0.7	ns
5	+5.6	0.0000	-1.3	0.0084	+1.8	0.0001
6	+1.1	0.0031	+0.1	ns	+0.6	0.0019
7	+1.2	0.0197	-0.2	ns	+1.7	0.0000
8	-1.3	0.0051	-2.8	0.0000	-1.7	0.0000
11	+0.6	ns	-4.6	0.0000	-3.0	0.0000
12	+2.0	0.0002	-0.6	ns	+1.3	0.0000
13	+0.9	0.0008	-1.6	0.0000	-0.5	ns
14	+3.1	0.0000	+3.2	0.0000	+2.8	0.0000
15	+1.5	0.0000	+1.6	0.0000	+1.6	0.0000
16	+1.2	0.0002	-0.7	0.0013	+0.4	ns
18	+0.7	ns	-2.0	0.0000	-1.0	0.0002

* Numeration used by Lavrov 1981 as in table 3 and figure 3.

natural immigrants were found to be very phenetically similar.

Metric differentiation of the skull was found to be considerable when some subpopulations of reintroduced beavers were compared with a subpopulation of natural immigrants. Thus, essentially the same pattern of relationship among subpopulations was found for both the phenetic and genetic analyses.

The most unexpected finding was that skulls of Lithuanian beavers were found to be significantly larger than those of beavers from the basic maternal population from the Dnepr basin, Belarus. According to skull size, Lithuanian beavers are much closer to beavers from the Voronezh region, Russia. The latter are considered to be the largest among other geographical forms/subspecies of *Castor fiber* (except for *Castor fiber albicus*).

Our investigations on morphology and genetics of a successfully restored hybrid population of European beaver in Lithuania show the quite complicated morphological and genetic structure of this population, which seems to be strongly related to the different origins of separate subpopulations. Significant changes at morphologic level might be one of the possible expressions of the potential survival advantage of hybrid populations.

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References

Balodis, M.M. 1990. The beaver. Biology and management in Latvia. Zinatne Publications, Riga, Latvia. (In Russian with English summary)

Beljakov, V.V., A.M. Balajan, Y.M. Romanov 1980. Results of the European beaver reacclimatization in Kaliningrad Region. Abstracts of the 6th Beaver Conference, Voronezh, Russia. (In Russian)

Halley, D.J. & F. Rosell 2002. The beaver's recon-

quest of Eurasia: status, population development and management of a conservation success. Mammal Review 32: 153-178.
Hartman, G. 1994. Ecological studies of a reintroduced beaver (*Castor fiber*) population. Reports of Department of Wildlife Ecology, Swedish University of Agricultural Sciences 25: 1-34.
Jablokov, A.V. & N.I. Larina 1985. Introduction into population phenetics. A new approach to study natural populations. Vysshaja shkola Publications, Moscow, Russia. (In Russian)
Kudriashov, V.S. 1975. On regulation of beaver abundance dynamics in the Oka Reserve. Proceedings of the Oka State Reserve 11: 5-125. (In Russian)
Lavrov, L.S. 1981. Palearctic beavers. Voronezh University Publications, Voronezh, Russia. (In Russian)
Macdonald, D.W., F.H. Tattersall, E.D. Brown & D. Balharry 1995. Reintroducing the European beaver to Britain: nostalgic meddling or restoring biodiversity? Mammal Review 25 (41): 61-200.
Mickus, A. 1988. The beaver. In: J. Prūsaitė (ed.). Fauna of Lithuania. Mammals: 100-106. Mokslas Publications, Vilnius, Lithuania. (In Lithuanian with English summary)
Nitsche, K.-A. & K. Pachinger 2000. Status, expansion, and perspectives of the beaver (*Castor fiber*) population in Slovakia. Game and Wildlife Science 17 (3): 165-176.
Paulauskas, A. & A. Ulevičius 2001. Genetic variability of European beaver (*Castor fiber* L.) in Lithuania. In: A. Czech & G. Schwab (eds.). The European beaver in a new millennium: 73-84. Carpathian Heritage Society, Krakow, Poland.
Rogers, J.S. 1972. Measures of genetic similarity and genetic distance. Studies in Genetics 7 (7213): 145-153.
Safonov, V.G. 1966. Morphological peculiarity and structure of beaver population. Bulletin MOIP, Biology LXXI (4): 5-19. (In Russian with English summary)
Saveljev, A. & A. Milishnikov 2002. Biological and genetic peculiarities of cross-composed and aboriginal beaver populations in Russia. Acta Zoologica Lituanica 12 (4): 397-402.
Solovjov, V.A. 1991. Beaver of north-eastern Europe. Leningrad University Publications, Leningrad, Russia. (In Russian)
Soule, M.E. & G.P. Zegers 1996. Phenetics of natural populations. V. Genetic correlates of phenotypic variation in the pocket gopher (*Thomomys bottae*) in California. Journal of Heredity 87 (5): 341-350.
Svendsen, G.E. 1989. Pair formation, duration of pair-bonds, and mate replacement in a population of beavers (*Castor canadensis*). Canadian Journal of Zoology 67 (2): 336-340.
Ulevičius, A. 1992. Phenetical structure of the beaver population in Lithuania. In: A. Kirk, A. Miljutin, T. Randveer (eds.). Proceedings of the First Baltic Theriological Conference, Tartu, Estonia: 120–132. Tartu Ülikool, Tartu, Estonia.
Ulevičius, A. 1993. Formation and spatial-phenetical structure of beaver (*Castor fiber*) population in Lithuania. PhD-thesis. Institute of Ecology, Vilnius University, Vilnius, Lithuania.
Ulevičius, A. 1994. Spatial-phenetic relations in the beaver (*Castor fiber*) based on different nonmetrical trait complexes. Ekologija (Vilnius) 2: 3-10. (In Russian with English summary)
Ulevičius, A. 1997. Beaver (*Castor fiber*) in Lithuania: formation and some ecological characteristics of the present population. In: K. Pachinger (ed.). Proceedings of the First European Beaver Symposium, Bratislava, Slovakia, 15-19 September 1997: 113-127. Comenius University Publisher, Bratislava, Slovakia.
Ulevičius, A. 1999. Density and habitats of the beaver (*Castor fiber*) in Lithuania. Proceedings of the Latvian Academy of Sciences, Section B. 53 (2): 101-106.
Ulevičius, A. 2001. Temporal changes in a high density beaver (*Castor fiber*) population. In: A. Czech & G. Schwab (eds.). The European beaver in a new millennium: 63-72. Carpathian Heritage Society, Krakow, Poland.
Vasil’ev, A.G., V.N. Bol’shakov, Y.M. Malafeev & E.A. Valyaeva 1999. Evolutionary-ecological processes in *Ondatra zibethicus* L. populations during acclimatization to northern conditions. Russian Journal of Ecology 30 (6): 399-406.
Zhivotovsky, L.A. 1979. Population similarity measure for polymorphic characters. Journal of General Biology (Moscow) 40 (4): 587-602. (In Russian with English summary)

Samenvatting

Over de morfologie en genetica van een succesvol herstelde beverpopulatie in Litouwen

Tenminste zes verspreidingscentra van uitgezette of langs natuurlijke weg geïmmigreerde dieren hebben de opbouw van de huidige beverpopulatie in Litouwen beïnvloed. Fenotypische

(niet-metrische schedelkenmerken) en genetische (allozyme electrophorese) analyses laten zien dat deelpopulaties van bevers van verschillende herkomst hun specifieke kenmerken behouden, ook in omstandigheden van grote populatiedichtheid, zelfs na 30 tot 40 jaar sinds de eerste uitzettingen en natuurlijke immigraties. Deze specifieke kenmerken kunnen het resultaat zijn van het zogenoemde *founder effect* in geografisch kleine en tijdelijk geïsoleerde groepen uitgezette dieren. Overigens, deelpopulaties van de veronderstelde zone van intensieve hybridisatie vertoonden uitwendig veel overeenkomst. Metrische schedelkenmerken varieerden in geringe mate tussen de deelpopulaties en vertonen een hoge differentiatie tussen uitgezette dieren en door natuurlijke immigratie verschenen dieren. Echter, beverschedels uit Litouwen bleken significant groter te zijn dan die van de oorspronkelijke populatie in de regio Gomel in Wit-Rusland. Onze onderzoekingen laten een gecompliceerde morfologische en genetische opbouw zien van de hybride beverpopulatie en aanzienlijke morfologische veranderingen in vergelijking met de oorspronkelijke populatie.

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Appendix

Similarity index and criterion of identity

The similarity index, which is the measure of phenetical similarity between two samples, and might be interpreted as frequency of joint morphs (phens, variants of non-metric trait) in both of these samples, has been defined as:

$$r = \sqrt{p_1q_1} + \sqrt{p_2q_2} + ... + \sqrt{p_mq_m},$$

where p_1, p_2, …, p_m are the frequencies of the m phens in the variability of the p-non-metric parameter for the first sample ($p_i<1$), and q_1, q_2, …, q_m are the frequencies of the same m phens in the variability of the q-non-metric parameter for the second sample ($q_i<1$). If the samples are compared by k non-metric parameters, then *r* is calculated as:

$$r = (r_1+r_2+…+r_k)/k.$$

The identity criterion, as a tool for evaluating of significance of phenetic distances, has been defined as follows:

$$I = 8n_1n_2(1-r-(p_0+q_0)/4)/n_1+n_2,$$

where n_1 and n_2 are the sizes of the samples compared; p_0 is sum of frequencies of phens that are presented in the first sample but not in the second one, accordingly q_0 is sum of frequencies of phens that are presented in the second sample but not presented in the first one. The identity criterion *I* is distributed as the well-known Chi-square criterion with the degrees of freedom *df* = m-1. By involving k non-metric parameters for the pairwise comparison of samples, *I* has been defined as:

$$I = I_1+I_2+…+I_k,$$

with the degrees of freedom calculated as:
$df = m_1+m_2+…+m_k-k$.