Long-term Dynamics and Morphological Peculiarities of Reintroduced Beaver Population in the Upper Volga Basin

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Abstract

Population of European beaver (*Castor fiber* L.) of the Upper Volga basin in the territory of Central-Forest Biosphere reserve has originated from eight animals relocated from the maternal Voronezh population in 1936–1937. At first decades, numbers of animals were initially in a state of depression and were characterized by the low quantity. Since the middle of 1970s, a drastic increase in population has started and reached more than 380 beavers in 2008. In accordance with the logistic equation model, the environmental carrying capacity is K=195 specimen. There was a saltation increase in the population density with r=0.227 transition from the first equivalent population conforming (27 specimen) since 1936 till 1971 to the second equivalent population conforming (195 specimen) from 1981 to the present. The rate of overall annual population increase is r=1.263±0.003 that is comparable to other reintroduced populations of European beavers. The significant correlation between oscillations in the population dynamic and climatic parameters was found.

Morphological appearances of the reintroduced animals significantly differ from the aboriginal ones in proportions of skulls (90% of correct classifications in the discriminant analysis) as well as in the non-metric parameters. The similarity/dissimilarity index on the polymorphic non-metric traits shows 3% of distinctions between populations. In the reintroduced population, an appreciably high fluctuating asymmetry of the epigenetic traits and higher coefficient of variation for metric parameters *versus* the maternal population has been found. In addition, more intensive ontogenesis processes in the reintroduced animals are shown. Such peculiarities may indicate a more intensive microevolution in the reintroduced population and adaptations to the new environmental conditions as well as the result of stochastic effects (genetic drift and fonder effect).

Key words: *Castor fiber*, reintroduced population, long-term dynamics, modelling, temperature, precipitation, morphological changes, epigenetic variability, fluctuating asymmetry

Introduction

The intensive and unattended harvesting of European beaver (*Castor fiber* L.) during XII – XVII centuries occurred and, as a result, entailed its number decrease in its natural habitat afterwards for insularity and progressing reduction of geographically isolated populations (Fedyushin 1935, Lavrov 1981). Only strict protection, organization of refuges and relocations saved beavers from disappearance (Zharkov 1969). Many decades since the relocations have passed, that allows us to evaluate today the project's success. Relocations of animals in many cases accelerate the microevolution processes in introduced populations that may be the cause of occurrence of the new morphological forms (Sjöberg 1996). Reintroduced populations are also convenient models for describing of invasion processes in the nature, especially on the background of long-term observation of population parameters. The reintroduced beaver population in the Upper Volga basin with well-known history of the origin, ecological-demographic parameters and collection materials is the congenial object for wide range researches.

The objective of the study is to quantify the reintroduced population size of *C. fiber* in the Upper Volga basin and to assess its ecological and demographic patterns and morphologic features in comparison with the maternal population. Another aim is to check the hypotheses about the influence of climatic variation on population relocated to the new environmental condition.

Materials and methods

The study area is situated in the Central Forest State Nature Biosphere Reserve in the centre of the European part of Russia. It is in the southern part of the Valdai Upland, on the Main (Caspian – Baltic) watershed of the East European Plain (Russia, Tver' region, Nelidovo and Andreapol' districts). Its coordinates are 56°26'– 56°39' north latitude, 32°39' – 33°01' eastern longitude (Figure 1).

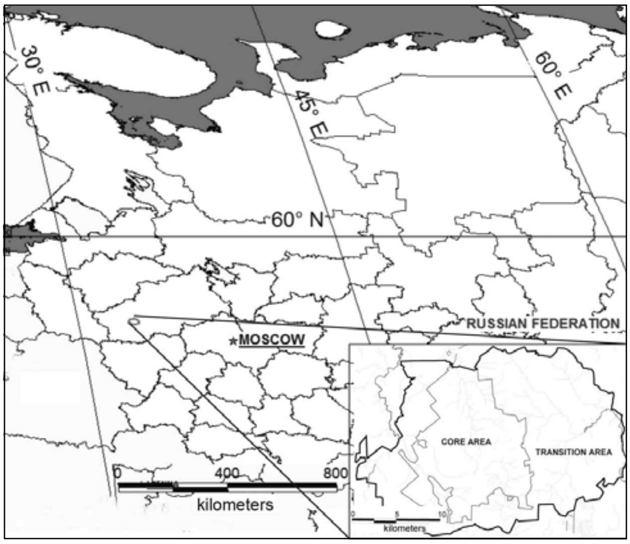

Figure 1. Study area location

The investigated part of the reserve constitutes 70,000 ha. It includes a core area of the Central-Forest Reserve (24,415 ha), and its transition area (46,061 ha). The status of Biosphere reserve the Central-Forest reserve obtained in 1985. Due to Seville strategy, its territory was divided into several parts. The biological and economic regime of the studied area varies from strictly protected (the Core area) to the managed forest area including clear cutting and hunting (the Transition area).

The landscape is a hilly moraine plain on the south-west part of the Valdai Upland with large upper peat bogs. The total area of bogs is 25% (Minaeva et al. 2001). The rivers of the Reserve are characterized by poorly developed, V-shaped narrow channels, and weak drainage facilities. Drainage density is 0.83 km/km^2 (Table 1).

Table 1. General information about main rivers in the study area

The river	Belongs to basin	The width of the channels, m*	The depth of the channels, m*	The length, km**	Stream current, m/s*
Tu'dma	Volga	2.5 – 12	to 2	36	0.08–0.4
Tudovka	Volga	4–20	to 2	38	0.1–0.4
Nochnaya	Tudovka	3–10	to 1.5	24	0.25–1
Tryasyanka	Tudovka	2–5	to 1	12	0.01–0.03
Zhukopa	Volga	1–9	to 1.5	16	0.015–0.1
Mezha	West Dvina	3–6	to 1	15	0.1–0.3

(*Yu. Efishin, 1983; **GIS "Zapovednik")

The average temperature of the last 60 years is +3.6 °C (min -50 °C, max +38 °C); the annual moisture is 740 mm (min 560 mm and max 950 mm). Long-term climatic data were obtained from meteorological station "Forest Reserve" (available as the database of the archive of Central-Forest reserve). Coordinates of the meteorological station are 56.45216 N and 32.97276 E. Average air humidity is 80%. Winds of the western direction prevail. The climatic conditions are quite typical for the moderate continental climate (Factors of regulation… 1983).

The ecosystem is typical of the south taiga subzone and represents a spatially expansive area of moraine relief in the central part of the east European Plain of Russia. The pristine south taiga spruce ecosystems survive here. The spruce (*Picea abies*) forests that dominates in the structure of the forests, covers 45% of the area. Pine forests (*Pinus sylvestris*) occupy 9% of the Reserve and are represented by waterlogged plant communities with low productive forest stand. Of the forested area, 27% is birch (*Betula* sp.) and 16% is aspen (*Populus tremula*), originated as result of succession processes after forest cutting, fires and windfall. Within the river valleys, alders (*Alnus glutinosa, A. incana*), and tillet (*Tilia cordata*) dominate, but occupy no more than 3% of the Reserve territory (Forest management of Central-Forest reserve 2007).

Data on beaver population dynamics were taken from Chronicles of Nature – annual records of conditions living and non-living surroundings of the reserves' territory (since 1961) and from published as well as unpublished historical records (store in Archive of Central-Forest Reserve). During the observation period of 1936-2008 three different methods of beaver counting were used: 1. Direct visual observations during the first decade after reintroduction (Aksenov 1960); 2. The statistical method of Khlebovich (1938), using a counting coefficient of 4 (starting at the end of 1940s). The method is based on counting of beaver settlements after multiplying the settlements by four (which is an average number of beavers in settlement for the European part of Russia). Regular counting of beavers started since 1947; 3. Estimation of beaver numbers in colonies by indirect attributes (used only after 2003) was performed by the methods of Lavrov (1952). After field reconnaissance, each settlement was placed into one of three groups: weak settlement: 1–2 beavers, medium settlement: 3–5 beavers, large settlement: >6 beavers.

Analyses of population dynamics are made using ecological modeling methods (Odum 1986).

The distribution of beaver's settlements is shown using a Geographical Information System (GIS) created in MapInfo using GPS information.

Morphological studies (metric and non-metric parameters) are based on beaver skull collections. Presented skull collections sampled in the local populations are mainly result of legal hunting or findings within the protected area. All studied skulls are of known sex. Age determinations were made using the Klevezal method (1988, 2007) by estimation of the cement strips on tooth roots for adult/senescent animals. For identification of age group of sub-adult animals, the shape of basal pulp cavity foramen was used. In additional for young animals less than one year old the Lavrov's method of age determination was used (Lavrov 1953). This method is based on stage development of deciduous teeth.

An example of the Aboriginal relict population representative of the Voronezh river basin (Voronezhsky Zapovednik, "VZ", n=85), sampling period 1975 – 1998, is stored in the Voronezh Biosphere Reserve. Reintroduced daughter population representative of the upper Volga basin (Central-Forest Zapovednik, "CFZ", n=120), sampling period 1982 – 1997 is stored in the Craniological laboratory of Central-Forest Biosphere Reserve. The total number of investigated skulls is 205.

15 metric parameters, including 7 bilateral which were measured on the both sides of the skull, were used (Figure 2). The accuracy of measurements is within 0.1 mm.

The morphological craniometrical divergence was investigated by analyses of variance (ANOVA), discriminant analysis and nonlinear estimation (Puzachenko 2004). Descriptive statistics is used to compare common biometrical constants. The analysis asymmetry of skull metric parameters was conducted using Zakharov's (1987) methods. The inter-population relations on the base of fluctuating asymmetry are made with ANOVA (Kozlov 2001).

In total, 22 non-metric traits included 69 phens of the European beaver skull that were used for phenotypic diversity analysis (Ulevicius 1988, Korablev et al. 1997). All characters occur bilaterally, and the traits were therefore registered on both sides of the skull separately.

1. Total length of cranium.
2. Rostrum length
3. Length of the nasal bone
4. Length of the upper teeth row
5. The diastema length
6. Width of the upper jaw (near foremen infraorbitalis)
7. Minimum interorbital width
8. Zygomatic width
9. Temporal width of the cranium
10. Mastoid width (between marginal points of *processus auricularis*)
11. Length of the lower teeth row
12. Total length of mandible (from *processus angularis* to leading edge of *incisors alveolus*)
13. High of mandible
14. Length of upper jaw
15. Length of mandible (from *processus articularis* to leading edge of *incisors alveolus*).

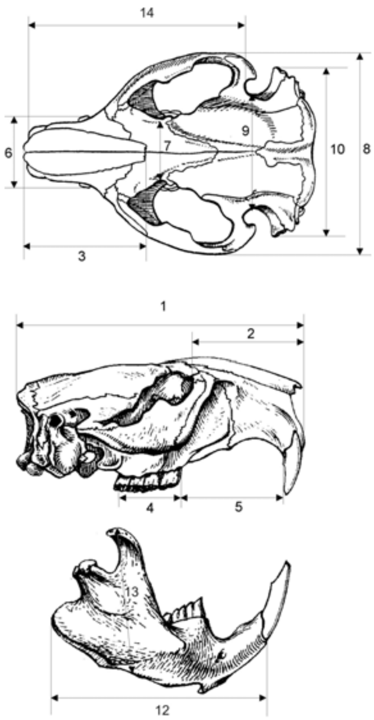

Figure 2. The scheme of skull measurements

Estimation of differences between maternal and reintroduced populations was made by cross tabulation method. Statistically significance of phens manifestation estimates was compared using Pearson chi-square. Zhivotovsky's (1982) method was used to evaluate level (*m*) and structure (*h*) of phenotypic diversity. Population similarity/dissimilarity measure for polymorphic characters was used for evaluation of non-metric distances (population similarity parameter, r).

Ontogenesis stability (Zakharov et al. 1996) was also analyzed . As an integral indicator of development homeostasis modification the fluctuation asymmetry level was used (medium frequency of asymmetric display on a sign, in percentage).

Results

The initial population of Central-Forest reserve was 5 animals. The founder group consisted of 3 adult females and 2 adult males taken from a maternal population in Voronezh reserve. In September 1936, the relocated animals were released into the Tudma basin in the Core Area of the Central-Forest Reserve (Aksenov 1960). The next year 4 more beavers were released at the same location.

During the first years several beavers were killed by lynxes (*Lynx lynx* L.), thus population was kept to 8 animals (Scherbakov 1947, Yurgenson and Yurgenson 1951). The first decades after reintroduction population growth rate was low probably due to suboptimal habitats and predators pressure, mainly brown bear (*Ursus arctos* L.) (Yurgenson and Yurgenson 1951, Aksenov 1960). By 1949, 33–37 individuals in 10 settlements lived on the Reserve territory (Yurgenson and Yurgenson 1951).

From 1951 to 1960, the Central-Forest reserve was abolished and beavers' density decreased substantially as a result of poaching. In 1961, about 15 animals existed (Solovjev 1967). Over this decade, animals moved in centrifugal directions to adjusted territories on Tudovka basin.

In the 1960s, the population was in a state of depression and had only a modest growth rate. At the beginning of the 1970s, growth rate grew exponentially. Since the middle of the 1980s , the population' density has increased, albeit with significant oscillation.

Long-term dynamic of the population in relations with external and internal parameters

The observation time period with intervals lasted for 73 years (1936-2008). Within the observation period, the population increased from 3 colonies (8 beavers) in 1937 to 84 colonies (348 beavers) in 2008 (Figure 3).

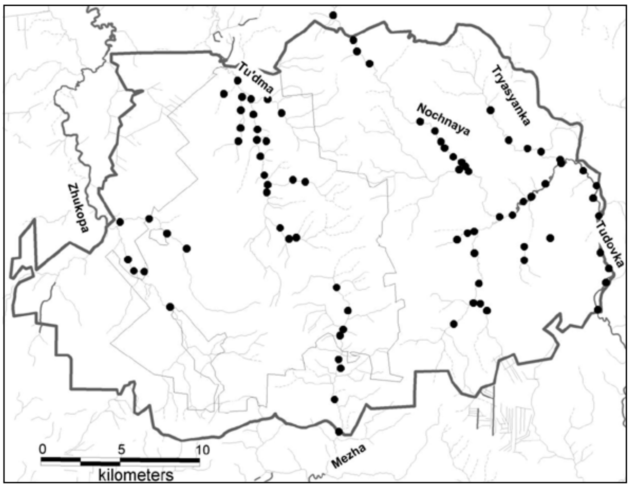

Figure 3. Distribution of beaver's settlements (black dots) on protected area of the Central-Forest Reserve in 2008

The long-term dynamic of the beaver population can be expressed with the classical logistic model:

$$N_t = \frac{rN_0 e^{rt}}{r + bN_0(e^{rt} - 1)}$$

where: r = rate of natural increase, b = coefficient of self inhibition, N_0 = initial population parameter, N_t = number of beaver at time point t. Parameters of this model are N_0= 0.0042, r=0.35, b=0.0018. The environmental carrying capacity K is 199 individuals with R^2=0.795.

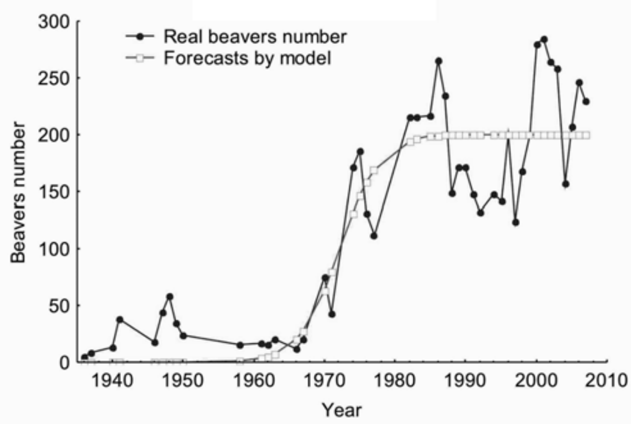

Figure. 4. Actual and estimated (see eq. 1) beaver population since reintroduction of 5 individuals in 1936

The model gives an initial population parameter of less than one animal. The consequence is that it does not have physical meaning. Apparently, step change of population parameters in the period from 1965 to 1980 does not correlate with an autochthonic dynamic.

At the next stage, model of population dynamics with discrete time (R^2=0.86) is given:

$N_{t+1}=N_t+ rN_t-bN_t^2=(1+ r)N_t-bN_t^2$.

Parameters of this model are r=1.263±0.0028, b=-0.0013±0.00001, p<0.0000.

The meaning of basic ecological parameters in this model is generally close to the logistic model: rate of natural increase r=0.263, coefficient of self inhibition b=0.0013, environmental carrying capacity K=193 specimens. The first equivalent population conforming (Figure 4) is about 10 animals, which is close to the actual founder number, i.e. N_i=8 beavers.

Figure 6 gives the real population dynamics and forecasts for the model with discrete time. This model fairly accurately predicts with real oscillation (relation of population density in the time point t to the time station t+1), with the exception of 2000-2003 (Figure 6). Hence, it is theoretically predicted in population dynamics models spasmodic transition with slight changes of external or internal parameters.

Essential is the fact that sensitivity of the new state of population has been reduced in relation to spring temperature falls and high flood power. It may be presumed that for the last 30 years population autocyclic fluctuations have been formed.

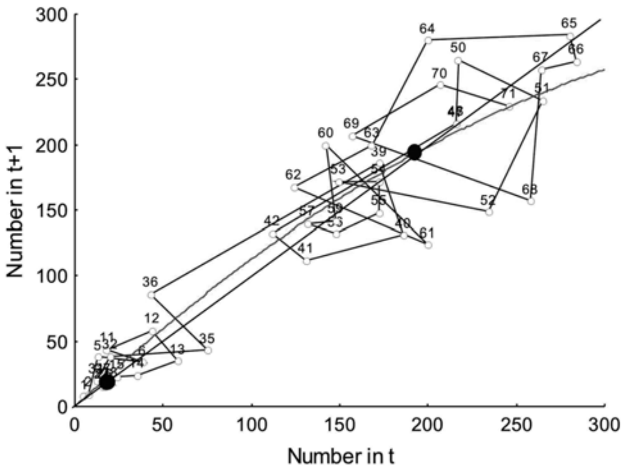

Figure 5. The diagram of population dynamic with time lag (Lamerey diagram). Black dots indicate the first and the second population conditions conforming

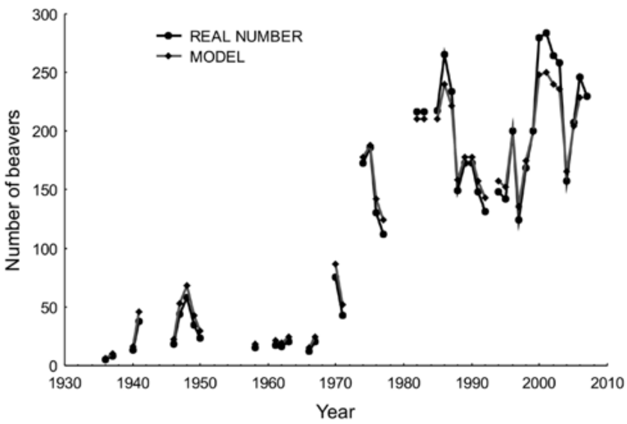

Figure 6. Quality of the model with discrete time

In accordance with Lamerey diagram, two classes of the population conforms are distinguished: low – less than 100 specimens, high – more than 100 specimens, so it is possible to use discriminantó analyses. The discriminate variables are monthly mean temperature and monthly total precipitation. The results of analysis significantly discern two population conditions (Table 2).

Table 2. Matrix of correct classification population conditions in relation to climatic variables $\chi^2 = 23.29$

Population density	Percent - Correct	1 - p=0.5070	2 - p=0.4930
Low	72.22	26	10
High	77.14	8	27
Total	74.6	34.0	37.0

Two variables have major weight: mean temperature in March (F=23.40) and total April precipitation (F=10.35). Low density of beavers is associated with combination of low temperature in March and high precipitation in April. In contrast, high beaver density is associated with combination of high temperature in March and low precipitation in April (Figure 7).

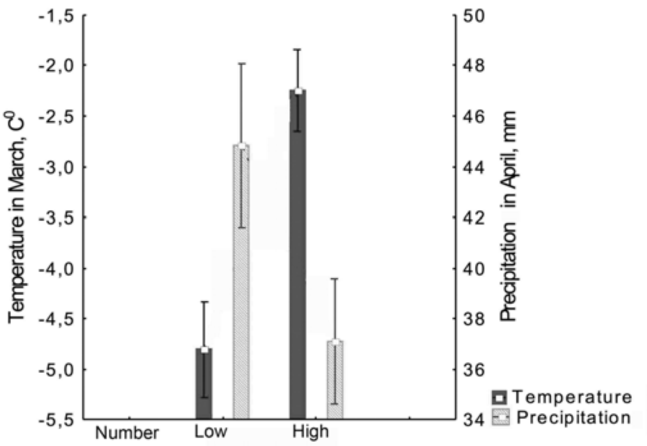

Figure 7. Influence of main climatic variables

Statistical analysis shows that the mentioned transition is, first of all, determined by March and April growing slightly warmer with corresponding drop of flood power. Accordingly, step increase in the beaver population during the 1970s is a cumulative result of auto-cyclic fluctuation, as well as low change of external parameters. Some reduction of spring flooding evidently promotes an increase in natural growth rate due to reduction of death rate that provides an increase of population to equilibrium quantity (from 10-25 to 200 animals). (Figures 5 and 7).

Craniometrical differentiation

At the first stage of investigation it is principally important to determine sexual dimorphism of beaver's skulls. For this purpose, all skull measurements were compared with a one-way ANOVA. Results confirm absence of sexual cranium differences (F=0.005–0.55; p=0.46–0.94) in all measured metric signs, meaning that cranium samples can be further tested without sex segregation.

Comparative analyses of ontogenesis skull growth for the VZ and CLZ populations were investigated with nonlinear estimation modelling. The logarithmical model for skulls growth used is:

$$y = b0+b1\times\log(x),$$

where y – is the sign (measurement), b0 - is the initial parameters (for the age less than one year) in mm; b1 – is the growth coefficient (shows the relative growth rate through all the age groups), and x – is age (within accuracy of one month, for the age less than one year or a half of year for adult animals). For the reason that of animals harvested during the hunting season (mainly from the end of October until December) young age groups include beavers with similar age in the VZ and CLZ samples. In total this model explains 70% of age-related changes at beaver skulls. First, with one-way ANOVA, separate measurements with strong dependence on age were made. Eight signs, describing integral (length, width) shape of skulls with F=9.9–59.8; p<0.001, were found.

Table 3. Mean (± error) of skulls initial parameters in aboriginal and reintroduced population (mm)

Sign	VZ (n=14)	CLZ (n=58)
Skull length	125.9±2.0	121.3±0.9
Length of lower jaw	90.8±1.6	87.9±.0.6
Zygomatic width	90.6±1.7	87.5±.0.6
Total length of lower jaw	99.0±1.6	96.1±.0.7
High of lower jaw	56.7±1.2	53.9±.0.4
Rostrum length	55.6±1.1	53.2±.0,4
Mastoid length	72.4±1.8	66.4±0.5
Length of upper jaw	97.4±1.5	98.7±.1.3

Results showed (Table 3) that juvenile beavers from the VZ population are characterized by larger skulls than those from CLZ, with the exception of length of upper jaw. Differences in the initial skull size between populations were significant (t =3.8; p =0.007).

Table 4. Skull growth (± standard error) metrics in aboriginal (VZ) and reintroduced (CLZ) populations (mm)

Sign	VZ	CLZ
Skull length	7.7±1.2	12.3±0.7
Length of lower jaw	5.9±1.0	9.7±0.5
Zygomatic width	5.9±1.0	9.8±0.6
Total length of lower jaw	6.3±1.0	9.5±0.6
High of lower jaw	3.3±0.7	6.7±0.4
Rostrum length	3.5±0.7	7.3±0.4
Mastoid length	2.9±1.1	7.7±0.5
Length of upper jaw	5.9±1.0	-*

* not estimated because not enough measurements in each age group for this measure

Growth rate of reintroduced beavers is higher in all of investigated measurements than that of the aboriginal population (Table 4). Such impressive distinction of growth coefficient is confirmed by statistical significance (t =17.76; p >0.0001).

It is nearly impossible to distinguish inter-population variability on the base of separate metric traits; therefore a multivariate statistic approach is preferred (Boeskorov and Puzachenko 2001).

Pre-selection of signs with greater resolution values is made with ANOVA. In all cranium proportions of VZ and CLZ, populations are found to be significantly (p<0.01) different. Results of measurement processing make it possible to distinguish two groups of signs: dynamic and conservative. The dynamic signs of skulls are characterized by high value of Fisher's criterion (F=11.5–91.6), which describes general proportions and allows discovery of morphological characters of each population more reliably. This group includes the following signs (relation VZ/CLZ, mean ±error, mm): skull length (142.6±0.66/141.0±0.79), rostrum length (63.3±0.37/65.0±0.45), length of upper jaw (109.5±0.56/99.0±1.69), zygomatic width (102.9±0.51/103.2±0.55), total length of lower jaw (112.4±0.58/111.0±0.66), mandible high (63.1±0.34/64.0±0.37). Conservative signs have a low value of Fisher's criterion (F=6.8–10.6) and with low-grade geographic variability contain: length of upper teeth row (34.0±0.17/34.0±0.19), inter-orbital width (27.9±0.20/28.4±0.17), temporal width (49.1±0.18/49.6±0.21) and almost the rest.

Analysis has shown transformation of general skulls proportions in reintroduced population. In comparison with maternal population, for decades after reintroduction (that is about 20 generations) skulls of CLZ beavers are characterized by longer and narrow rostrum, shorter of maxilla length, larger zygomatic width, short and high mandible.

Multivariate inter-population metric variability was explored with discriminant analysis. Measurements with F–criterion < 10 (pre-selection with ANOVA) were removed from discriminant model; among them were the most conservative signs. Beaver weight is insufficient to identify geographical intra-specific variation. Forward stepwise analysis with F 3.5 to enter and 3.4 to remove selected five variables with the maximum discrimination of Wilks' Lambda criterion 0.3–0.4. Classification matrix shows 90% of correct identification for the both populations. Much better recognition is observed for VZ beavers with a probability of 95%, while the CLZ population is correctly observed only for 86%. Three measurements have the biggest weight for recognition of beavers from different populations: i) rostrum length; ii) length of upper teeth row; and iii) width of upper jaw (VZ/CLZ 29.3±0.21/28.7±0.27 mm). Results of discriminate analysis give the evidence, on the one hand, of deep morphological differentiation; on the other hand, of similarity with maternal population.

Mean coefficients of variation for integrative characteristic of intra-population variability for all signs were calculated in accordance with Yablokov (1966). The mean for all measurements was VZ=3.92±0.20% (min 2.81–max 5.46) and CLZ=4.43±0.52% (min 2.85–max 11.2). Coefficient of variation in reintroduced population certainly is greater, but not significantly, considering standard error.

In many bilateral measurements, direct asymmetry (sum of left minus right sides) was found. On skulls from maternal population cumulative dextrad asymmetry for the sign length of lower teeth row was confirmed (Sum_{l-r}=14.3; P=99.9). Samples from reintroduced population are characterized by left side cumulative asymmetry for all measurements except mandible high and length of lower teeth row. The relation of direct asymmetry with geographic origin of population is investigated using a one-way ANOVA. For two signs: rostrum length and length of lower teeth row connection are confirmed (F= 4.2–13.7; p<0.000). Hence, one attribute of maternal population dextrad asymmetry for the reintroduced population is the left side asymmetry.

In skull samples from the reintroduced population, two traumas (1.7%) and one pathology case (0.9%) were found. Traumas were injury of zygomatic bone on the left side with synostosis and oblong foramen between maxilla and nasal bones probably was a result of bite by beaver's incisor. One skull of senex beaver was found with deforming arthrosis of *caput mandibulae* and *facies articularis*.

Non-metric (phenotypic) variability

Investigations of epigenetic variability as characteristic of separate phens manifestation based on variations frequency are made. To evaluate epigenetic variability, 69 phens are selected. Manifestation does not depend on sex and age of animals, which is confirmed by cross-tabulation comparison (χ^2=0.008 – 10.95; p>0.05).

Frequency of occurrence of some dominant non-metric traits reaches 40% between examined samples. For example, traits of *USOs Character unionis ossium squamosi et occipitalis (sutura brevus)* occurrence in maternal population on 63% of skulls in reintroduced population is found to be only of 20%. Traits of *FSTm Dispositio fissurae sphenotimpanicae et suturae squamoso-sphenoideae (medialis)* are 98% and 67%, respectively. Traits of *CFOf Configuratio fissurae orbitalis (septa filiformium)* occurrence in maternal population is of 47% of skulls in reintroduced population constitutes 28%.

To evaluate the dynamics of phenotype, reintroduced population samples are divided into three groups: CLZ 1 (n=33, the birth period 1973–1984); CLZ 2 (n=34, the birth period 1985–1989); and CLZ 3 (n=36, the birth period 1990–1996). The dynamics of phen's frequencies in reintroduced population are closely related to the birth period of the animals. In many cases, the precise tendency of their increase or decrease concentration is visible. Three most variable traits are shown in Table 5.

Table 5. Frequency of variable non-metric traits in reintroduced population

Traits code	CLZ 1	CLZ 2	CLZ 3
USOs	0.28	0.19	0.13
*FPAs**	0.94	0.82	0.46
CFOf	0.15	0.27	0.36

* FPAs – *configuratio foraminis canalis palatini anterioris vario sine septis*

The presence of significant population differences according to frequencies of phen's manifestations shows that more than 90 % of non-metric parameters differ in populations. Maximum values in populations' differences have seven mostly polymorphic traits (χ^2=14.7–167.1 with high significant probability level). Level (μ) and structure (h) of phenotypic diversity are calculated for all non-metric traits of both population and are shown in Table 6.

Table 6. Characteristic of level and structure of phenotypic diversity

	VZ		CLZ	
	μ	*H*	μ	*h*
Limits min–max	1.280–3.902	0.004–0.549	1.199–3.672	0.004–0.600
Mean ± error	2.134 ± 0.123	0.256 ± 0.082	2.119 ± 0.114	0.249 ± 0.035

The mean level of phenotypic diversity was statistically the same in maternal and reintroduced populations. After reintroduction in CLZ population, the phenotypic diversity slightly decreased as well as structure of phenotypic diversity. The pair VZ–CLZ Zhivotovsky's similarity/dissimilarity index was r=0.97±0.01 (mean for the all non-metric traits) with high probability level (W=0.001). This means that phenotypic fund of maternal and reintroduced populations are quite similar. However, populations could be considered as separate groups of animals with 97% of common phens.

Fluctuating asymmetry was found in all non-metric bilateral traits. The highest level of fluctuating asymmetry occurred in polymorphic traits with more than two variations. Mean of asymmetry for these ten traits is 24.4±0.83%. For all investigated non-metric characteristics, the mean of fluctuating asymmetry in the VZ and CLZ populations were 11.7±1.9% and 27.5±3.4%, respectively. In addition, distinction of fluctuating asymmetry appearance was present (t =7.04; p<0.000).

Discussion and conclusions

Analyses of reintroduction efforts showed that in cases where beavers were relocated to small groups in spacious areas, populations increased for 40 years

(Zurowski and Kasperczyk, 1988). A similar situation occurred in Central-Forest reserve. A limited number of founders combined with suboptimal environmental conditions, and pressure from predators and humans in first decades after reintroduction resulted in a stable but low population density. However, in the study period, beavers colonized many rivers and streams both in core area and adjusted territories. The further adaptation to the new surroundings contributed to spasmodic increase of population density. As the population is located mainly on a protected territory, and there is only very limited hunting on the transition area, our results support our initial hypothesis that population growing is determined by variation of external variables and first by all climate changes.

Autochthon oscillation of population density is generally influenced by spring climatic variation – specifically temperature and precipitation. Physical meaning of such correlation with decrease of spring flooding is that it insures better safety of dams. Negative influence of extreme spring or autumn flooding on beaver settlements is shown in the North of Russia (Teplov 2004) in Washington, USA (Müller-Shwarze and Sun 2003) and in New Brunswick, Canada (Mitchell and Cunjak 2007). Physical effects of floods are - breached or destroyed beaver dams and food supply.

On the other hand, climatic factors may carry more complex influence on artificial (relocated) populations. The climatic variation, especially in spring period, determines quality and nutrition of food for herbivores, this factor closely connected with reproductive facilities of animals, as well as with the period of copulation (Nolet et al. 2005). We suggest that climate is the most strong factor that influences populations in many dimensions.

Other important factors that have a strong influence on beaver dynamics, are windfalls and predators pressure. Huge windfalls occasionally occur in Central-Forest reserve, thus increasing complex mosaic structure and refuge capacity of habitats. Beaver form an important share in diet of lynxes, wolves and bears. The subsequent research will show whether predators exercise regulatory influence on population size.

In relation to other cases, that were known, the comparison with reintroduced population of European beaver in Latvia is interesting (Balodis 1990). In this population, the rate of annual natural increase (r) varies from 1.16 to 1.63 (the mean 1.25) that were more low theoretically expected value (2.16), because in nature population self-inhibition mechanisms exist, such as underestimated time of generation, and considerable quantity of not breeding females. In Biesbosch region (the Netherlands), the growth rate of relocated population was extremely low (0.75) due to very low reproduction while in Labem district (Czech Republic) population with the similar history was characterized by high growth rate (2.03) (Nolet et al. 2005). Rates of population increase of beavers in two local study areas in Sweden were 1.7 and 2.9, respectively (Hartman 1994). Hence, birth rate of reintroduced population in Latvia is quite similar to the population in Upper Volga Basin.

As for population density, our data suggest that 0.13 of settlements/sq.km in The Central-Forest reserve is not a limit for the climax beaver's population. For example, in the climax reintroduced population of The Prioksko-Terrasnyi Reserve average density of beavers is 0.44 settlements/sq.km (Zavyalov et al. 2010). The density of old reintroduced Sweden population of beavers at the end of the XXth century was 0.21 settlements/sq.km (Hartman 2003). Probably relatively low beaver's density in The Central-Forest reserve is due to real environmental capacity.

As it was shown in previous work (e.g., Milishnikov et al. 1997, Ulevicius 1997, Paulauskas and Ulevicius 2001, Ulevicius and Paulauskas 2003, Saveljev 2003) morphological peculiarities of reintroduced beaver populations differ from aboriginal (maternal) populations because of the founders' effect and narrow bottleneck due to relocation. Reintroduced population of beaver in The Central-Forest reserve and adjacent territories forms clear "Voronezh" lineage from a very limited number of founders. What can be supposed about skull morphology specificity of colonists after more than five decades? The results of investigation show that descendants distinguish from maternal group by complex changes in ontogenesis characteristics, as well as metric and non-metric conditions. Rapid-growth of reintroduced beavers' population from Russian European North in comparing with Voronezh beavers were shown by Solovjev (1991). He considers this specificity as adaptation to severe north conditions. Evidently, the beavers of The Central-Forest reserve are of rapid growth – a characteristic, occurring probably because of rapid population density growth. Hence, this ontogenesis type of invasive population is a singularity. Skull morphology changes in metric dimensions are statistically significant but not discrete. For example, there was found deeper divergence between maternal Berezina population and its daughter's populations from Desna, Cheka and Chertola rivers (Korablev 2008). At all, morphological appearance of Voronezh beavers is more conservative compared to Berezina beavers on the base of skull measurements. Some changes in length and width of upper jaw as well as rostrum, probably have occurred in the reintroduced population due to a stochastic founder effect as well as a result of genetic drift. The possible functioning adaptation of these changes must be investigated in further researches on more wide comparative material.

Coefficient of variation in both populations was moderate, confirming previous findings. For example, skull coefficient of variation for the beaver population from Vyechegoda River (northeast of Russia) was 2 – 4% (Solovjev 1991), and was similar for aboriginal Berezina population (Byelorussia) (Stavrovskij 1986).

Cumulative direct asymmetry of skulls is characteristic of both populations. Similar tendencies are shown for other mammals' species, for example, in several localities of sea, for otter (*Enhydra lutra nereis)* skulls (Barabash-Nikiforov 1962, Aryan 1993). Most probably, the reason is the connection with prevailing dextral or sinistral animals in specific population as ancestral feature of group founders. The reason is asymmetrical signs for connection with jaw apparatus, which reflects the tendency for chewing on the left or right side of the denture.

Non-metric analyses of skulls revealed structure divergence between maternal and reintroduced population on the basis of phenotypic fund. Obtained value of phenotypic diversity level (*m*) was less than the ones for nine geographic localities of European beaver from Lithuania (Ulevicius 1997). Phenotypic diversity levels were *m*=2.33–2.64/ 2.12–2.13 in Lithuania/ Central-Forest and Voronezh Reserves, respectively. Relatively high *m* is connected with cross-translocation and natural immigration origin of Lithuanian beavers. Probably, due to narrow bottleneck in reintroduced population of The Central-Forest reserve, the level and structure of phenotypic diversity is low. Particularly, general number of phens has lowered by 7. Obviously, lthe evel of phenotypic diversity is related to founder number and their heterozygosity.

The value of similarity/dissimilarity measure demonstrates comparatively low microevolution changes in reintroduced populations. One the other hand, it corroborates formation of phenotypic fund in framework of maternal population and its clear origin without influence of possible immigrants.

Impaired physiological conditions, resulting from frequent anomalies traumas and pathologies, are not evident in the reintroduced population. Odontology anomalies, which are a sign of inbreeding, are absent (Bouwmeester et al. 1989, Saveljev 1989, 2003).

Fluctuating asymmetry could be considered as a measure of ontogenesis stability (Zakharov 2001). In some cases, the level of fluctuating asymmetry indicates inbreeding processes in discrete populations, originated from limited founders (Wayne et al. 1986, Conception et al. 1995, Rautian et al. 1998). Level of fluctuating asymmetry in reintroduced population of beavers is not critical in comparison with other semi-aquatic mammals. For example, the level of fluctuating asymmetry in isolated population of European mink (*Mustela lutreola* L.) at The Central-Forest reserves' area was 39% (Korablev et al. 2002). Low level of fluctuating asymmetry of beaver's craniums from the Voronezh Reserve can be explained by the following reasons: a) animals were not relocated; b) stable high density of population during several decades; c) absence of extreme climatic factors influence (Nikolaev 1997). Increase of fluctuating asymmetry in reintroduced population can be explained by: a) relocation into new environmental conditions that provokes "environment's stress"; b) by passage through narrow "bottle neck"; c) by inbreeding in the isolated group; and d) by influence of limiting environmental factors (Istomin 1994, Zakharov 2001).

Considering our results, we suppose that reintroduction of European beaver in the Upper Volga basin is very successful. The viable CLZ population originates from limited founders' number and demonstrates absence of inbreeding depression signs. Results, presented here, have confirmed Milishnikov's (2004) estimation of extremely low N_e for beavers in this area, likely due to poor environmental conditions.

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МНОГОЛЕТНЯЯ ДИНАМИКА ЧИСЛЕННОСТИ И МОРФОЛОГИЧЕСКИЕ ОСОБЕННОСТИ ПОПУЛЯЦИИ БОБРОВ РЕИНТРОДУЦИРОВАННЫХ В БАССЕЙНЕ ВЕРХНЕЙ ВОЛГИ

Н. П. Кораблев, Ю. Г. Пузаченко, Н. А. Завьялов и А. С. Желтухин

Резюме

Популяция европейского бобра (*Castor fiber* L.) Верхневолжского бассейна (территория Центрально-Лесного государственного природного биосферного заповедника) происходит от 8 животных транслоцированных из аборигенной воронежской популяции в период с 1936 по 1937 годы. Численность бобров в первые десятилетия после выпуска находилась в угнетенном состоянии. Интенсивный рост численности популяции начался в середине 1970-х годов, и к 2008 году численность в пределах охраняемой территории достигла 380 бобров. В соответствии с логистическим уравнением емкость среды оценивается в 195 особей. Однако вследствие чрезвычайно низкой начальной численности N_0=0.011 лишена физического смысла. Имеет место скачкообразное изменение численности (моментальный коэффициент размножения r=0.227) с переходом от первого равновесного уровня численности в 27 особей (1936 – 1971 годы) ко второму уровню равновесной численности в 195 особей (1981 год по настоящее время). Средний ежегодный прирост популяции составил r=1.263±0.003, что сравнимо с другими реинтродуцированными популяциями европейского бобра. Обнаружена значимая корреляция между флуктуациями численности популяции и значениями климатических параметров в весенний период.

Морфологические особенности размерных и дискретных признаков достоверно отличают бобров Центрально-Лесного заповедника от аборигенной воронежской популяции (90% корректной классификации в дискриминантном анализе). Также реинтродуценты характеризуются более интенсивными онтогенетическими изменениями размерных признаков черепа. Морфологические особенности, отмеченные у реинтродуцированных бобров, могут быть связаны с микроэволюционными процессами и адаптацией к новым условиям обитания, а также являться следствием случайных факторов, таких как дрейф генов и эффект основателя.

Ключевые слова: *Castor fiber*, реинтродуцированная популяция, долговременная динамика, моделирование, температура, осадки, морфологические изменения, эпигенетическая изменчивость, флуктуирующая асимметрия