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Patterns of Population Dynamics of Eurasian Beaver (*Castor fiber* L.) after Reintroduction into Nature Reserves of the European Part of Russia

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Abstract—This paper presents the results of analysis of the population dynamics of Eurasian beaver after its reintroduction into the Lapland, Darvinsky, Central-Forest, Prioksko-Terrasnyi, Oksky, and Khopersky natural reserves that are located in European Russia in the northern, southern and central parts of the beaver range. The paper analyzes the effectiveness of a discrete time model that includes a feedback between animals and their food resources for the quantitative description of the population dynamics in the optimal, suboptimal, and pessimal habitats. It is shown that the beaver population dynamics demonstrates four grows types (patterns): the eruptive type (Lapland Reserve); single-stage type with a quasi-periodic oscillation (Prioksko-Terrasnyi Reserve), multi-stage type with quasi-periodic oscillations (Darvinsky, Central-Forest, and Khopersky reserves) and the logistic curve of population growth with periodic oscillations around it (Oksky Reserve). The biotic and abiotic factors that determine these types of animal population dynamics are discussed.

Keywords: reintroduction, population dispersal, Eurasian beaver, ecosystem engineering activity, population dynamics, mathematical model, prediction

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INTRODUCTION

By the early 20th century, Eurasian beaver (*Castor fiber* L.) almost disappeared in most parts of Eurasia. The recovery of the Eurasian beaver population in the Soviet Union was mainly due to the large-scale works in the 1950–1970s on intentional introduction of the beaver into its historical range (reintroduction) in a number of regions (Zharkov and Sokolov, 1967; Zharkov, 1969; Dezhkin et al., 1986). It is estimated that the intensity of reproduction of beaver populations in the restored range varied from 4.5% of the average annual growth in the northern taiga regions to 32% in mixed forests in the west of European Russia (Lavrov, 1975, 1981). Baskin et al. (2011) showed that the dynamics of the recovery of the beaver populations changed with a geographical latitude. By 1972–2003, the beaver population density reached 0–1.4 beavers to the square km in the southern regions (48°–55.5° N), 0.1–3.3 beavers to the square km in the middle latitudes (56°–59.5° N), and 0.04–1.1 beavers to the square km in the northern latitudes (60°–63.5° N). While in 1972 there was no statistically significant difference in the beaver population density in regions of different latitudes, the population densities of the northern and middle latitudes as well as northern and southern latitudes significantly differed as early as 1991 and 2003, but there was no significant difference in the indicators of beaver population density at the middle and southern latitudes. Currently, Eurasian beaver numbers are growing due to beavers colonizing unoccupied watercourses and growth in the density of earlier formed populations (Grevtsev, 2011). In 2011, the total beaver population in Russia was 600000–650000 (Borisov, 2011).

Studies of beaver followed its recovery; yet, the ecological consequences of reintroduction and patterns of beaver populations growth still remain insufficiently studied. Some success was achieved by analyzing the state of beaver populations in natural reserves, since the places of release, number, sex, and age of released animals were known in those cases; population protection and survey were organized, and the environment was monitored.

In recent years, the importance of natural disturbances of different types for the dynamics of forest ecosystems and preservation of biological diversity is understood more and more (Smirnova, 2004; Bobrovskii, 2010). The sources of such disturbances include Eurasian beaver as a keystone species (an edificator species, ecosystem engineer) that transforms aquatic and riparian ecosystems, which abound in forest landscapes (Zavyalov et al., 2005; Zavyalov, 2015). That being said, the role of beavers in the structure and dynamics of forest ecosystems is still insufficiently studied. This is especially important for the countries of Western Europe and Russia, where, owing to the programs for beaver reintroduction and subsequent population dispersal, Eurasian beaver is restoring its former positions in aquatic and riparian ecosystems (Grevtsev, 2011; Halley et al., 2012; etc.).

An effective method to describe, analyze, and predict the main trends of beaver population dynamics in different environmental conditions is to create special mathematical models. However, the models that are traditionally used in ecology are not always suitable for the study of beaver populations, since they take into account the trophic relationships and competition of species, but do not include the influence of a species on a habitat and the feedback between a species and its environment. For example, the classical "predator–prey" model of Lotka-Volterra or its modifications (the Rosenzweig–MacArthur model) for prey, predator, and super-predator, for the most part include trophic relationships and species competition (Deng, 2001). The researches (Cuddington and Hastings, 2007; Petrosyan et al. 2012a; *Rechnoi bobr kak klyuchevoi*..., 2012) showed that it was not correct to use these models as well as modified discrete models of Malthus, Beaverton-Holt, and Ricker and models based on the time series analysis to describe the population dynamics of key species that actively change their environment. Such species may have higher population growth rates in suboptimal and pessimal habitats than other.

In addition to general descriptions, there are several main models that were developed to predict the influence of key species on riparian ecosystems. For example, Gurney and Lawton (1996) developed a model for the situation when the role of a key species is to modify the habitat and move it from one state into two–three others. The research by Cuddington and Hastings (2004) showed that the non-equilibrium dynamics of key species differed from the dynamics of non-key species, making it difficult to predict their population dynamics and distribution. Wright et al. (2004) used a model that assumed the following: at the moment t E individuals can use the total habitat stock $T = H + V + D$ that is composed of usable habitats (H—active habitats), recovering habitats (V), and those, which are temporarily unsuitable for beavers (D—degraded habitats). The used system of differential equations reflects changes in the values of H, V, and D in time with consideration for the following parameters of the intensity of changes in habitats: r—the rate of colonizing new habitats, p—the rate of transition from the state V into H; d and c—the rates of degradation and recovery of habitats, respectively. The models that are presented in this work are designed to make long-term prediction, but the use of a continuous time scale creates certain difficulties in interpreting the results. To overcome this, we developed a discrete time model that was used to describe beaver population dynamics for the Prioksko-Terrasnyi Biosphere Nature Reserve (Petrosyan et al., 2012b).

The goal of this work was to establish the patterns of beaver population dynamics under different environmental conditions on the basis of the available long-term data. The tasks of the study included the following: the quantitative characterization of the development of beaver populations from introduction to the present time in cases of specially protected natural areas (reserves); identification of the main trends and patterns of beaver population dynamics in the reserves that are located in different natural zones of Russia; and predicting the state of populations of this key species.

MATERIALS AND METHODS

We analyzed the data on the long-term beaver population dynamics in the area of six reserves that are located in European Russia: the Lapland, Darvinsky, Central–Forest, Prioksko–Terrasnyi, Oksky, and Khopersky Reserves (Fig. 1). The data on beaver population dynamics were published earlier with the exception of observations in the Khopersky Reserve (see below).

The Lapland Reserve (LR) is located in the mountainous regions of the Kola Peninsula, to the north of the Arctic Circle (67°39′ N, 32°38′ E). The area of the reserve is 276 435 ha. It is confined to the hypoarctic (taiga) type of mountain altitudinal zonality (Fig. 1). Most of the territory (55%) is covered with northern taiga forests composed of pine (*Pinus sibirica* Du Tour; *Pinus friesiana* Wichura), spruce (*Picea obovata* Ledeb.; *Picea fennica* (Regel) Kom.), and birch (*Betula callosa* Lindq.; *Betula kusmisscheffii* (Regel) Sukaczev; *Betula pendula* Roth). The forest plant communities also include rowan (*Sorbus gorodkovii* Pojark), gray alder (*Alnus incana* (L.) Moench), goat willow and two-color willow (*Salix caprea* L.; *Salix phylicifolia* L.), and small groups of aspen (*Populus tremula* L.).

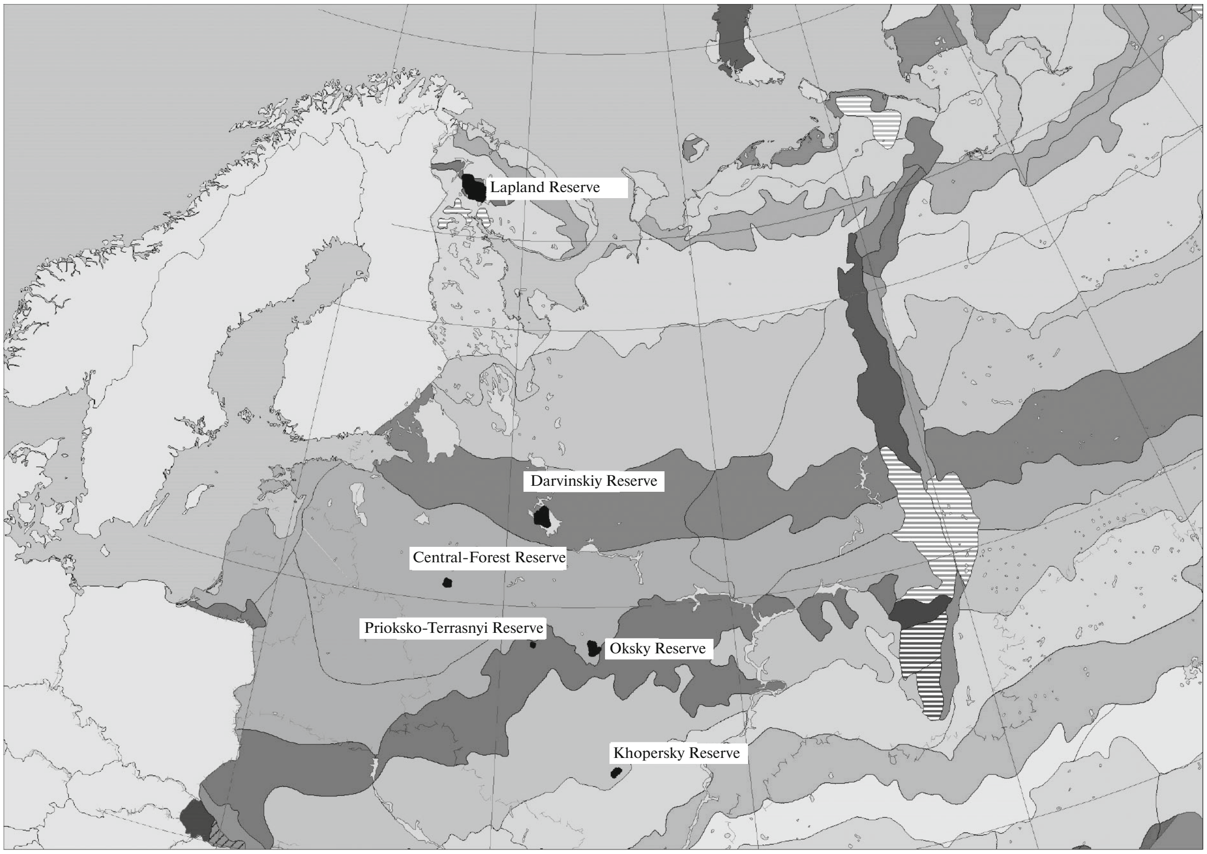

Fig. 1. Location of the studied reserves: Lapland Reserve—the hypoarctic (taiga) type of mountain altitudinal zonality; Darvinsky Reserve—the subzone of southern taiga; Central-Forest Reserve—the subzone of subtaiga; Prioksko-Terrasnyi Reserve—the area in the transition zone between sub-taiga and broad-leaved forests; Oksky Reserve—the subtaiga subzone; Khopersky Reserve—the forest steppe subzone. The names and boundaries of plant cover items are given according to (Ogureeva et al., 1999).

The hydrological network of the reserve includes lake and river systems and several rivers from sources to mouths (*Zapovedniki*..., 1998).

The reintroduction of Eurasian beaver in the reserve began in 1934. An analysis of beaver population dynamics in the reserve was carried out using the data of surveys from 1934 to 1985 (*Rechnoi bobr* ..., 2012). Some results of the primary analysis with the use of the classical models models were presented earlier (*Rechnoi bobr* ..., 2012; Goryainova et al., 2011).

The Darvinsky Reserve (DR) is located in the south-taiga forests of the Mologa-Sheksna Lowland (58°28′–58°50′ N, 37°29′–38°10′ E) (Fig. 1). The south-eastern edge of the lowland is flooded by the Rybinsk reservoir to the mark of 102 m above sea level. The area of the reserve is 112673 ha. Open marshes constitute more than 27% of the reserve terrestrial part. Forests in the reserve are confined to riverbanks. Pine forests (*Pinus sylvestris* L.) are prevalent (73.5%). Birch forests (*Betula pendula* Roth) account for 19.6%, spruce forests (*Picea abies* (L.) Karst.) account for 5.2%, the share of aspen forests (*Populus tremula* L.) is 1.3%, and the share of black alder forests (*Alnus glutinosa* (L.) Gaertn.) is 0.4%. Forests on excessively moistened soils account for about 70% of the reserve forested area. The first gnowings of settling beavers were noted in the territory of the reserve in August 1976 (Zavyalov et al., 2005).

The beaver population dynamics in the territory of the reserve was analyzed using the surveys data from 1980 to 2001 (Zavyalov et al., 2005).

The Central-Forest Reserve (CFR) is located in the south-western part of the Valdai Hills within the main Caspian-Baltic watershed of the Russian Plain (56°26′–56°39′ N, 32°39′–33°01′ E), in the sub-taiga zone (Fig. 1). The area of the reserve is 24415 ha. The territory is typical moraine landscapes of the Upper Volga region. The vegetation communities are dominated by indigenous forests composed of spruce (46%), pine (9%), and black alder (1%). Oligotrophic and mesotrophic sedge marshes occupy 4% of the reserve area. Derivative forests of downy birch (*Betula pubescens* Ehrh.), aspen, and gray alder were formed as a result of windfalls, decomposition of overmature stands, and partially due to deforestation in the period of liquidation of the reserve in 1951–1961. These forests occupy about 40% of the territory (*Struktura i produktivnost'* ..., 1973). The density of forest rivers and streams is about 0.75 km per square kilometer of the reserve area. Most of them form part of the Tyudma River basin.

In 1936–1937, four pairs of beavers from the Voronezh Reserve were released into the reserve (Korablev et al., 2011, 2012). The locations of beaver sites and the population size for 1936–2001 were presented according to the materials of the Nature Chronicle of the Central-Forest Reserve. The archival data from the Nature Chronicle for 1936–2001 had been preliminarily processed and presented for the analysis by V.V. Bobrov. The data for 2001–2010 was taken from the research by Korablev et al. (2011).

The Prioksko-Terrasnyi Reserve (PTR) is located on the left bank of the Oka River (Moscow oblast) (54°51′–54°55′ N, 37°34′–37°41′ E) and is in the transition zone between sub-taiga and broad-leaved forests. The area of the reserve is 4945 ha, of which 93% are occupied with mostly middle-aged forests. Pine forests (*Pinus sylvestris* L.) (40%) and birch forests (*Betula pendula* Roth, *Betula pubescens* Ehrh.) (35%) are prevalent. Among other woody species, a noticeable role is played by aspen, spruce, oak (*Quercus robur* L), lime (*Tilia cordata* Mill), and black alder. Grasslands make up 1.5% of the territory. Prior to the establishment of the reserve, its territory was subjected to intensive human activity, which, together with biotopic heterogeneity of the territory, determines the high patchiness of the modern plant cover in the reserve (*Atlas* ..., 2005). The hydrological network of the reserve is represented by rivers, lakes, and swamps. The main watercourses cross the reserve from north to south. These are two forest rivers with systems of broad gullies and ravines with streams: the Ponikovka that is about 6 km long and the Tadenka that has a length of 8.7 km, of which 6.5 km are in the territory of the reserve. The basin of the Tadenka River is now home to 60–85% of the beaver population in the reserve (*Rechnoi bobr* ..., 2012).

In 1948, after nearly 400 years of absence (Smirnov et al., 2000), two pairs of beavers from the Voronezh Reserve were released in the Tadenka middle reaches. The beaver population dynamics was analyzed using the surveys data from 1948 to 2010. A detailed description of the methods for collecting survey data and its preliminary analysis were presented in a number of publications (Zavyalov et al., 2010; Petrosyan et al., 2012b; *Rechnoi bobr* ..., 2012).

The Oksky Reserve (OR) is located in the central part of European Russia, in the south-eastern part of the Meshchera Lowland (54°40′–55°0′ N, 40°35′–41°0′ E). Its area is 55744 ha. In addition to typically outwash landscapes of the Meshchera Lowland, the territory of the reserve includes the valley complex of the Oka River. The Oka is the basis of the hydrological network in the reserve. Other important components are the Pra River that flows into the Oka, numerous floodplain oxbow lakes, and non-inundated lakes. The reserve is in the south of the sub-taiga forest zone, but vegetation falls out of the zonal series. Forests are mainly formed by pine; they are replaced by black alder and birch forests in marshy lowlands and by oak groves along rivers (Pankova, 2012a, 2012b). The oxbow ponds of the Oka floodplain are rich in aquatic vegetation; there are vast willow thickets along banks (*Zapovedniki*..., 1998).

In 1937–1940, 23 beavers from the Voronezh Reserve were released into three floodplain lakes (Kudryashov, 1975). We used the surveys data from 1949 to 2010 for the analysis. The results of the preliminary analysis with the use of classical models were published earlier (Goryainova et al, 2011; *Rechnoi bobr* ..., 2012).

The Khopersky Reserve (HR) is located in the forest-steppe Khoper region that is confined to the south-eastern part of the Oka-Don Lowland (50°42′ N, 42°00′ E). The area of the reserve is 16200 ha. It stretches along the Khoper river in its middle reaches. The reserve includes low (1–3 m above the river level) and high (5.5 m) floodplains and an above-floodplain terrace with complex aeolian processes, as well as an elevated part that is 70–80 m higher than the Khoper level. There is a developed network of gullies and ravines (*Dubravy Khoperskogo zapovednika*..., 1976a, 1976b). The predominant width of the floodplain is 2–4 km. The Khoper floodplain includes about 400 water bodies of various areas, the largest of which have an area of 14–45 ha. Forests occupy 85.7% of the reserve area, floodplain oak forests are prevalent (48.2%), and black alder forests account for 15.8%. The elevated part accounts for 15.2% of the forest area.

In 1937–1939, 22 beavers were brought from the Voronezh Reserve to the Khopersky Reserve (Dyakov, 1975). The surveys data for 1975–2012 that had been obtained within the program of the Nature Chronicle were used for the analysis.

Methods for determining beaver population size. Three methods were used to count beavers in different reserves: an ecological statistical method (Dyakov, 1975), statistical method, and L.S. Lavrov's procedure (1952). These methods assess the number of colonies at the end of the year. The beavers number is obtained by multiplying the number of colonies by the average number of beavers in a colony. The ecological statistical method and Lavrov's method assign colonies to one of 3–4 groups, which differ in the number of beavers in a colony. The belonging of a beaver colony to a given group is determined by visual estimation using a specially developed scale (Lavrov's method) or by counting the total number of tree and shrub trunks cut by beavers; and by determining the amount of "relative food units," which in turn is an indicator of a colony size (Dyakov, 1975). In addition to autumn surveys, in the Khoperskiy and Oksky Reserves the surveys data was refined using the data of multiple beaver catches (Dyakov, 1975; Kudryashov, 1975). The number of colonies in the Oksky and Darvinsky Reserves was specified by special spring counts and visual observations (Kudryashov, 1975; Zavyalov et al., 2005).

Modeling of population dynamics. The original parametric and discrete-time (finite-difference) mathematical model of beaver population dynamics depending on time and availability of food resources was presented for the first time in the research (Petrosyan et al., 2012b). The potential of this model was demonstrated for the Prioksko-Terrasnyi Reserve case. The main assumptions of this model are:

(1) The total resource $R(t)$ does not change with time t during the studied time interval [0, T], that is $R(t) = R = \text{const}$.

(2) Like in the works (Wright et al., 2004; Petrosyan et al., 2012b), the total resource is composed of three components

$$R = R^{(a)}(t) + R^{(p)}(t) + R^{(d)}(t),$$

where $R^{(a)}(t)$, $R^{(p)}(t)$, and $R^{(d)}(t)$ are active, potential, and degraded food resources, respectively. The active resource is a resource that is available for consumption by beavers. The potential resource is a resource that is recovering from the degraded state and trasforming into an active resource. A decayed active resource changes to a degraded resource and then transforms into a potential resource.

(3) The recurrent expressions for determining beaver population $P\,(t_k)$ and value of active $R^{(a)}(t_k)$, potential $R^{(p)}(t_k)$, and degraded resources $R^{(p)}(t_k)$ at the moment t_k were described earlier (Petrosyan et al., 2012b).

In order to determine the parameters of the discrete model, stationary values of population dynamics P_s, and resources $R_s^{(a)}$, $R_s^{(p)}$, and $R_s^{(d)}$ as well as to analyze the stability of stationary solutions, we used the methods presented in the work (Petrosyan et al., 2012b). The population growth rate is defined in the work as the ratio of the subsequent beavers number to the previous one (P_{t+1}/P_t). Its value is more than 1 at the phase of population growth. The growth rates were estimated using both surveys data and the models.

RESULTS

The Estimate of the Parameters and Adequacy of the Model Based on Survey Data

The parameters and adequacy of the model that describes the beaver population dynamics and state of food resources were estimated using a special software (Petrosyan et al., 2012b). The study estimated the adequacy of the model based on the determination coefficient R^2 (Afifi and Eizen, 1979), the values of which range from 0 to 1. This coefficient indicates what proportion of the variability in a beaver population and resources can be explained (described) by the system of equations (1) (see Petrosyan et al., 2012b). The values of this coefficient that was calculated based on the discrete model for the studied reserves range from 0.62 to 0.99 (Table 1).

Table 1. Beaver population P_s, percentage of active R_a^s, potential R_p^s, and degraded R_d^s resources in the stationary state of the system for the studied reserves with the determination coefficient R^2

Reserve	P_s	R_a^s	R_p^s	R_d^s	R^2
LR	25.6	0.14	0.83	0.03	0.97
DR	713.5	0.007	0.45	0.543	0.99
CFR	316.7	0.001	0.367	0.632	0.62
PTR	42.28	0.012	0.598	0.39	0.86
OR	474.43	0.4208	0.2791	0.2991	0.73
KhR	780.8	0.022	0.429	0.549	0.84

The obtained values of the determination coefficient lead to the conclusion that the proposed model describes the beaver population dynamics adequately enough, given the relatively large ranges of actual data and absence of data on beaver numbers for some years. The beaver population dynamics is described best for the Darvinsky Reserve ($R^2 = 0.99$) and worst for the Central-Forest Reserve ($R^2 = 0.62$) (see Table 1).

Beaver Population Dynamics on the Basis of Observations and Modeling

The quantitative estimate of the beaver population dynamics and the population growth rate for the Lapland Reserve are given in Figs. 2a and 2b. The population dynamics can be generally described by three different time intervals. During the first interval from 1934 to 1954 with a duration of 20 years, there was a monotonic growth to 108 individuals. In the second interval with a duration of 28 years, there was a population decrease to 12. The third interval was notable for the stabilization of population at the stationary value of about 26 individuals. The population growth rate is on average 1.14 for the first interval, 0.95 for the second interval, and tends to the stationary value of 1 for the third interval (after achieving the value of 1.14 in 1982). The proportions of the active, potential, and degraded resources in the stationary state are 14, 83, and 3%, respectively (Table 1). The proportion of the resource that is at the stage of recovery (83%) is somewhat higher than that in the other studied reserves (Table 1). In combination with a large stock of food resources that is actively used by animals (14%), this leads to the conclusion that the small beaver numbers in the reserve are the result of the slow recovery of food resources.

The data on beaver population dynamics in the Darvinsky Reserve shows that there was a slow popu-

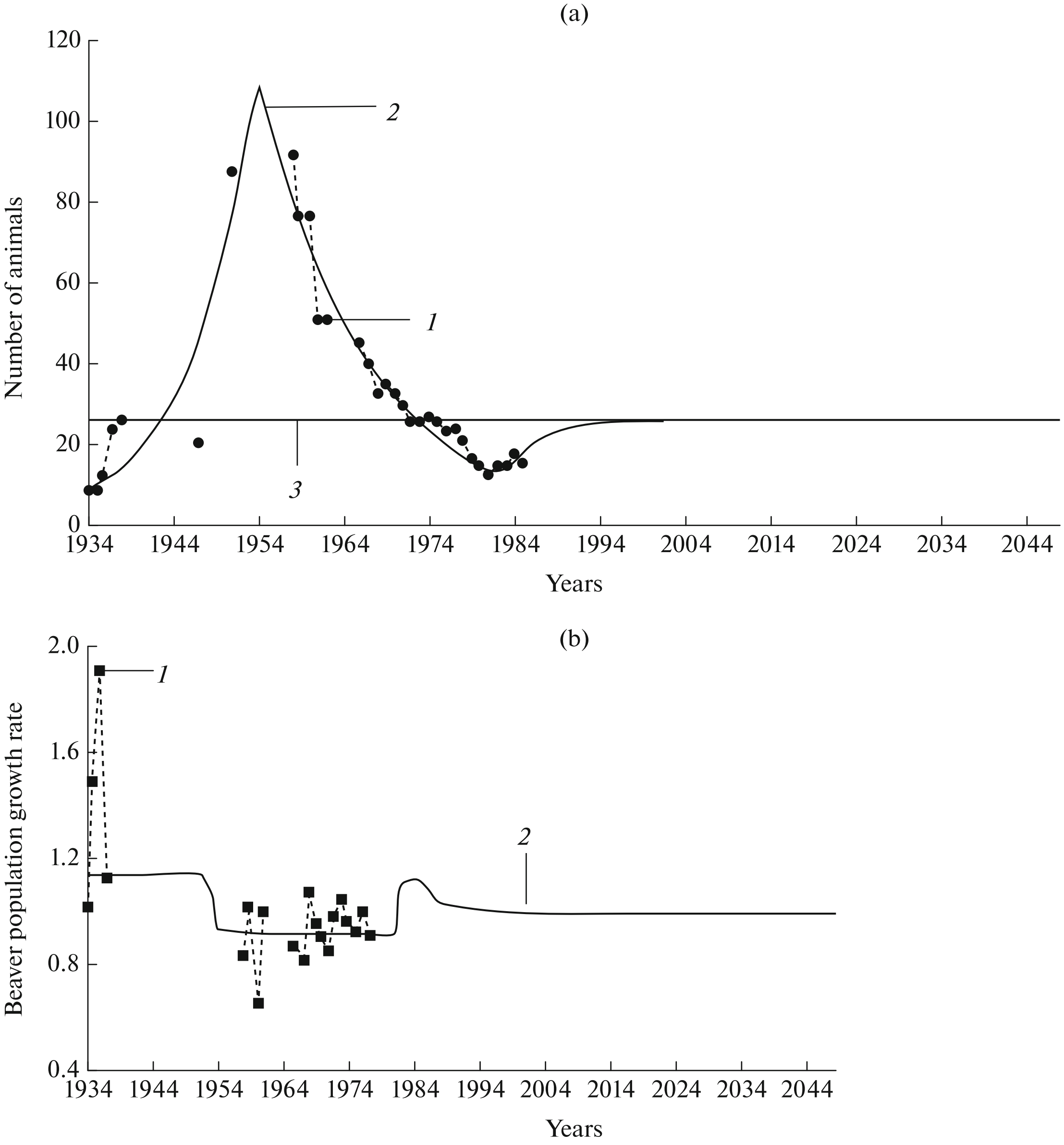

Fig. 2. (a) Beaver population dynamics in the Lapland Reserve (*1*—the survey data; *2*—model estimates; *3*—steady population). (b) Dynamics of the beaver population growth rate (P_{t+1}/P_t) in the Lapland Reserve (*1*—growth rate determined based on the survey data; *2*—its model estimate).

lation growth from the moment of reintroduction (in the late 1970s) to 1987, which was replaced by a rapid growth in the period from 1988 to 2015. The model estimate shows that the subsequent population changes will be characterized by a long oscillation at the high population level with 47 years period of quasi-periodic oscillation (see Fig. 3a). The graph of the dynamics of the population growth rate shows that its values began to abruptly decrease after reaching 1.75. According to the model estimate, the weak oscillations of the growth rate around the value of 1 are expected after 2020 (see Fig. 3b). The stocks of the active, potential, and degraded resources in the stationary state are 0.7, 45, and 54.3%, respectively (Table 1). The beaver population dynamics of the Prioksko-Terrasnyi Reserve tends to a steady state with a quasi-periodic component of 14–26 years (see Fig. 4a). The model estimate of the dynamics shows that the quasi-periodic component has a saw-toothed shape with the beaver population growing from the minimum to the maximum for the first 6 years of each period, and decreasing from the maximum to the minimum during the rest of a period (8–20 years) (Fig. 4a).

Figure 4b shows the graph of change in the beaver population growth rate. From 1968, the dynamics of the growth rate is a quasi-periodic function with a

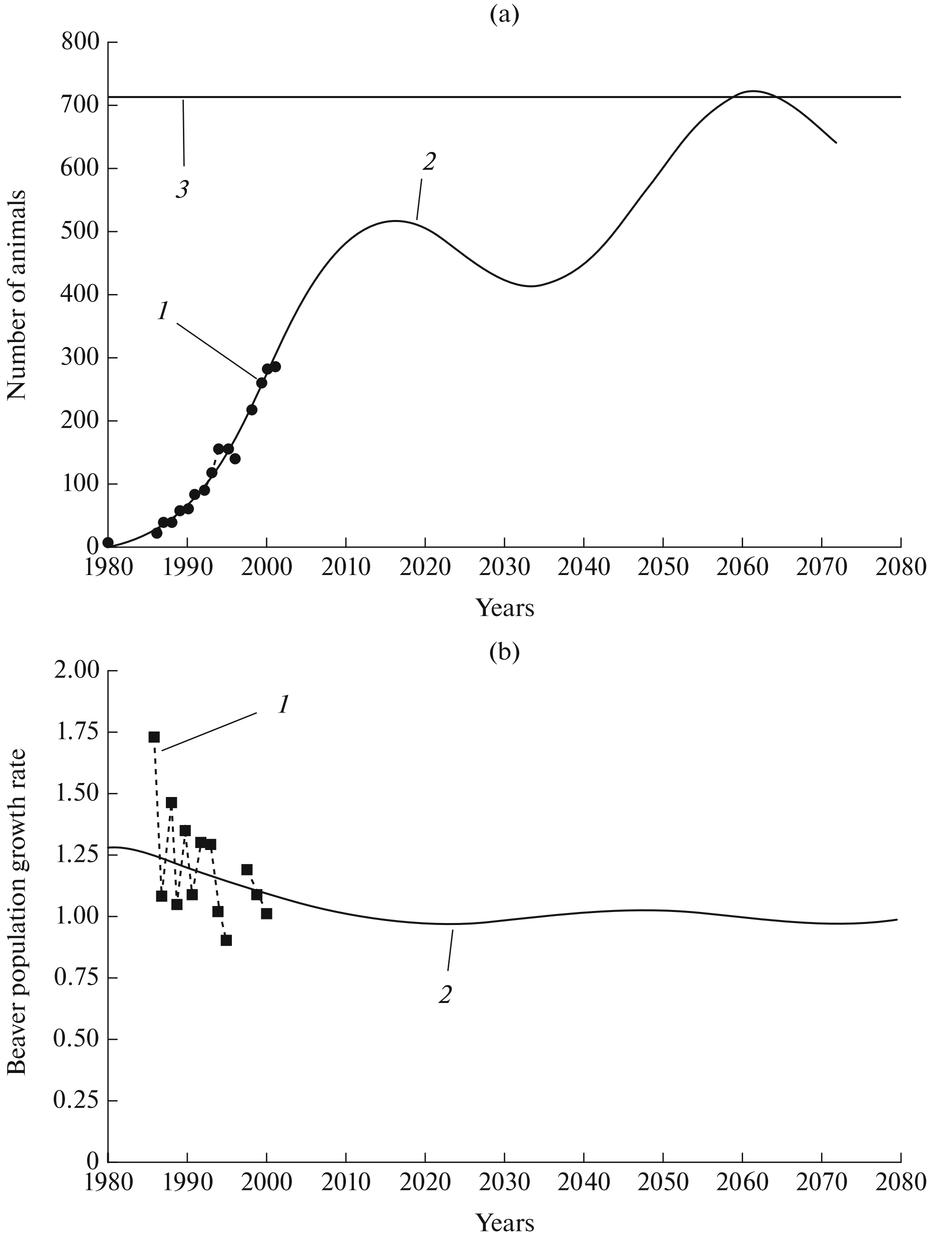

Fig. 3. (a) Beaver population dynamics in the Darvinsky Reserve (*1*—the survey data; *2*—model estimates; *3*—steady population). (b) Dynamics of the beaver population growth rate in the Darvinsky Reserve (*1*—growth rate determined based on the survey data; *2*—its model estimate).

period of 26 years. The growth rate has a maximum value of ~1.1 and minimum value of ~0.98. The phases with the values that are more than or equal to 1 last about 6 years, and those with the values that are less than 1 last 20 years. This means that the beaver population grows 3.3 times faster than it decreases. The stocks of the active, potential, and degraded resources were 1.2, 59.8, and 39% (Table 1).

The survey data and model estimates of the beaver population dynamics in the Central-Forest Reserve are presented in Figs. 5a and 5b. A slow population growth is observed from 1936 to 1954, and then there is a population growth to the maximum in 2001. A long-term oscillation at the high population level can be predicted at a later stage with a quasi-periodic oscillation of 84 years (see Fig. 5a).

Analysis of the dynamics of the population growth rate shows that it begins to decrease after reaching the value of 2.75 in 1946, and then its small oscillations around 1 are observed (see Fig. 5b). The proportions of the active, potential, and degraded resources in the stationary state are 0.1, 36.7, and 63.2%, respectively (Table 1). The value of the active resource stock is the lowest among those noted for the studied reserves, and

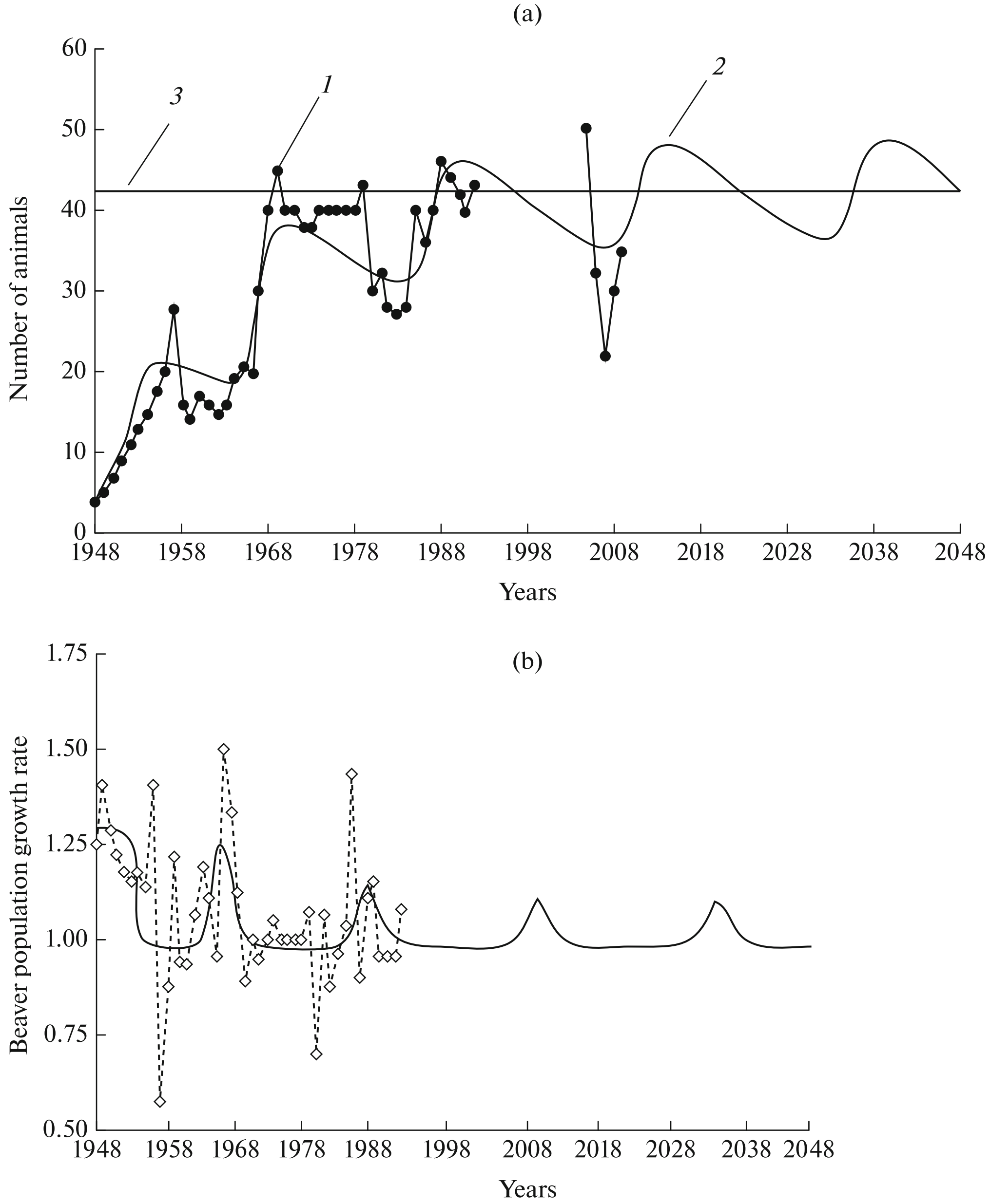

Fig. 4. (a) Beaver population dynamics in the Prioksko-Terrasnyi Reserve (*1*—the survey data; *2*—model estimates; *3*—steady population) (according to Petrosyan et al., 2012b). (b) Dynamics of the beaver population growth rate (P_{t+1}/P_t) in the Prioksko-Terrasnyi Reserve (*1*—growth rate determined based on the survey data; *2*—its model estimate).

the proportion of the degraded resource is the highest. However, the small stock of the potential resource (a lower value was obtained only for the Oksky Reserve) indicates its rapid transition into the active state, which is beneficial for the beaver population.

The survey data and model estimates of the beaver population dynamics and the rate of population growth in the territory of the Oksky Reserve are presented in Figs. 6a and 6b. In contrast to other reserves, the beaver population growth is described there by the logistic curve with some periodic oscillation (16 years period) around the growth curve. In other words, our model reveals some oscillation component of the beaver population dynamics in the reserve; at the same time, it correctly shows the presence of the logistic trend in this dynamics. To verify this assertion, the parameters of the logistic model that very accurately describes the trend of population change were found (see Fig. 6c). The determination coefficient (R^2 = 89.42%) indicates that the presence of the logistic trend of population growth explains this dynamics by approximately 90%. According to this model (Fig. 6c, curve *1*), the population size grows at the first stage rapidly enough, but then the population growth slows

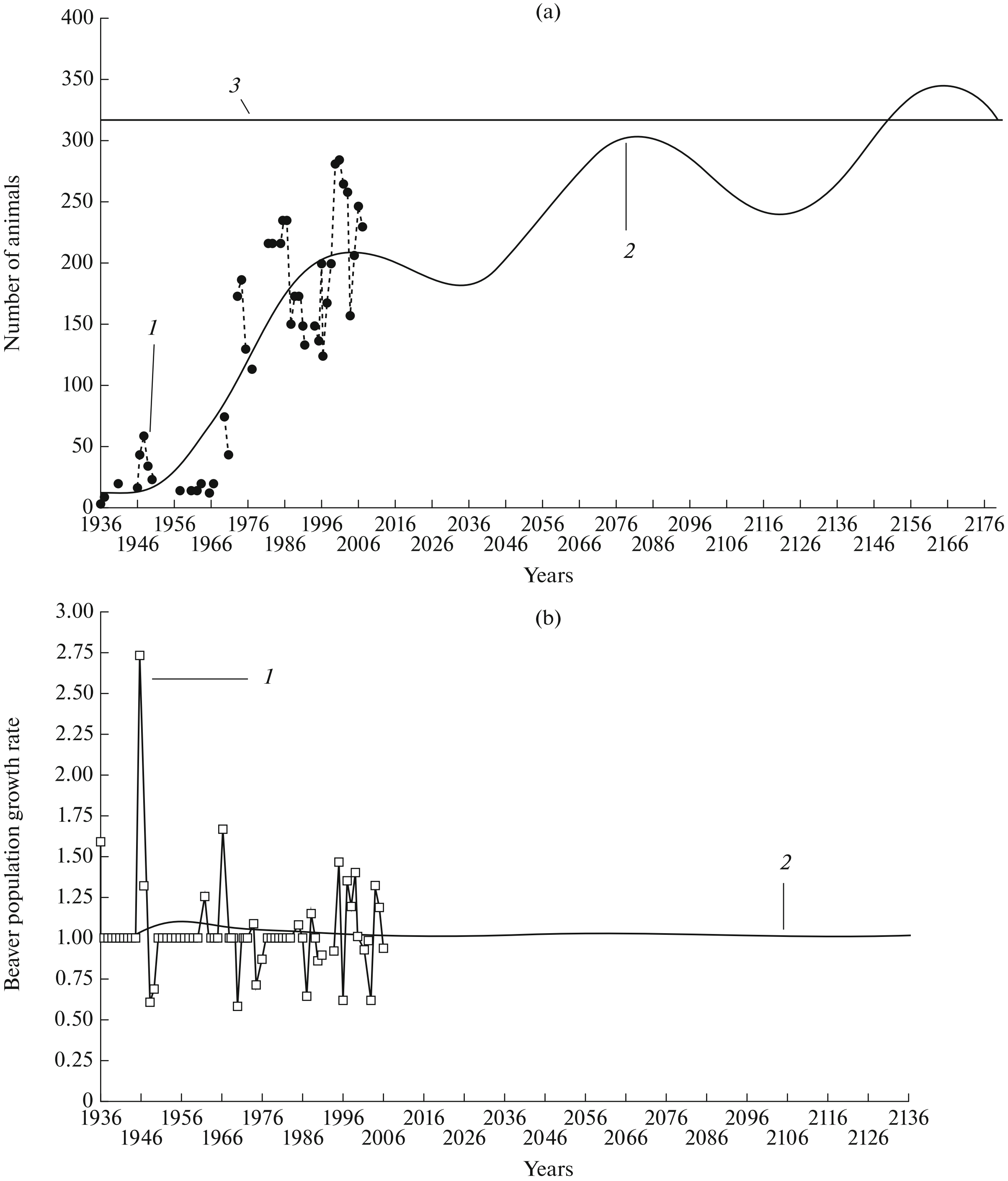

Fig. 5. (a) Beaver population dynamics in the Central-Forest Reserve (*1*—the survey data; *2*—model estimates; *3*—steady population). (b) Dynamics of the beaver population growth rate (P_{t+1}/P_t) in the Central-Forest Reserve (*1*—growth rate determined based on the survey data; *2*—its model estimate).

down and becomes infinitesimal near the value $K = 452$ individuals (that is, the logistic curve asymptotically approaches the stationary value). It also follows from these dynamics that the available resources (the active and potential resources) can ensure the long-term oscillation of population size around an established stationary value.

The graph of change in the population growth rate also indicates that this variable tends to the steady state after some oscillation. The stocks of the active, potential, and degraded resources in the steady state are 42, 28, and 30%, respectively (Table 1). For this reserve, the stock of the active resource is higher than for other five studied reserves, the stock of the potential

Table 2. Eigenvalues of matrix A that characterize the steady states of the system (see formula 8 according to (Petrosyan et al., 2012b))

Reserve	ρ_1	ρ_2	ρ_3	$\max\limits_{i=1,2,3} \lvert \rho_i \rvert$
LR	0.01	0.8019	0.3666	0.8019
DR	0.9899 – 0.131*i*	0.9899 – 0.131*i*	0.9759	0.9989
CFR	0.9988 + 0.07406*i*	0.9988 – 0.074*i*	0.9882	1.0015
PTR	0.9640 + 0.2868*i*	0.9640 – 0.2868*i*	0.9392	1.0058
OR	0.9166 + 0.3764*i*	0.9166 – 0.3764*i*	0.9643	0.9643
KhR	0.7409 + 0.2887*i*	0.7409 – 0.28876*i*	0.9732	0.9731

resource is the lowest, and that of the degraded resource is the highest, surpassing only the one calculated for the Lapland Reserve. This once again confirms that the living conditions in the Oksky Reserve are favorable for beavers.

The estimates of the population dynamics of Eurasian beaver for the Khopersky Reserve are presented in Figs. 7a and 7b. The stable growth in the beaver population was observed until the early 1980s; then it was followed by the decline that lasted until 1997–1998. The decline was replaced by a new rise and oscillations at the high population level. Analysis of the dynamics using model (1) shows that the 1957–2037 period is characterized by the 16-year cycle of quasi-periodic population oscillation (Fig. 7a). The graph of change in the population growth rate also shows periodic oscillation (Fig. 7b). The proportions of the active, potential, and degraded resources are 2.1, 42.9, and 54.9% (Table 1).

Analysis of the Stability of Steady Solutions

For the analysis, the eigenvectors ρ_1, ρ_2, ρ_3 of matrix A were calculated (see formula 8 (Petrosyan et al., 2012b)). These vectors characterize the steady states of the system of equations. Their values for each of the reserves as well as their maximums (in absolute value) are presented in Table 2.

Table 2 shows that the eigenvalues ρ_3 have real positive values for all the reserves, and eigenvalues ρ_1, ρ_2 that are expressed by complexly conjugated numbers are found for most of the reserves, except for the Lapland Reserve (Petrosyan et al., 2012b). For the Lapland Reserve, all eigenvalues (real numbers) are less than 1, so the steady solution is stable, and the periodic component is absent. The solution of the equations of population dynamics for the other five reserves has a periodic component. The reserves can be approximately divided into two groups. The first group includes the Darvinsky, Oksky, and Khopersky reserves, for which the steady solutions are stable: the maximum absolute values of the eigenvalues are less than 1 (the last column in Table 2). For the Prioksko-Terrasnyi and Central-Forest reserves, these values are more than 1, so the steady solutions are not stable. However, it was found that the unstability of the steady solution in a first approximation was rather low and had an oscillation (see Figs. 4a and 5a). The performed analysis of how the solution of the system of equations behaves at a rather large time interval (the time intervals of 1948–2050 and 1936–2136 were taken) showed that system's variables tend to limit periodic functions with time.

DISCUSSION

Our previous study (Zavyalov et al., 2015) presented the general conceptual model of the beaver population dynamics under different scenarios of the rate of recovery of food resources; however, it became necessary to conduct additional studies with the use of a special discrete model in order to obtain a more detailed picture of the recovery of population in different conditions. The use of the proposed model is important because it includes the feedback between animals and their habitats that makes it possible to identify the quasi-periodic pattern of the dynamics and to make the prediction estimates of population size for 30–50 and more years. In general, based on the beaver population dynamics that are presented in Figs. 2–7, we can assert that the discrete model allows identification of the general trends and patterns of animal population dynamics in different natural conditions.

In this work, in order to interpret the results of the beaver population dynamics, we distinguish single-stage and multi-stage patterns with quasi-periodic oscillations as individual types in addition to the eruptive and logistic patterns, which have been described sufficiently well in the literature. We understand the single-stage patterns with a quasi-periodic oscillation as the animal population dynamics, in case of which the achievement of the maximum value is followed by population oscillations around this threshold value. In case of the population dynamics of key species, the single-stage model shows the rapid achievement of the limit of possible changes (modification) in habitats as a result of the activity of these species and formation of the feedback system that prevents the further environmental changes.

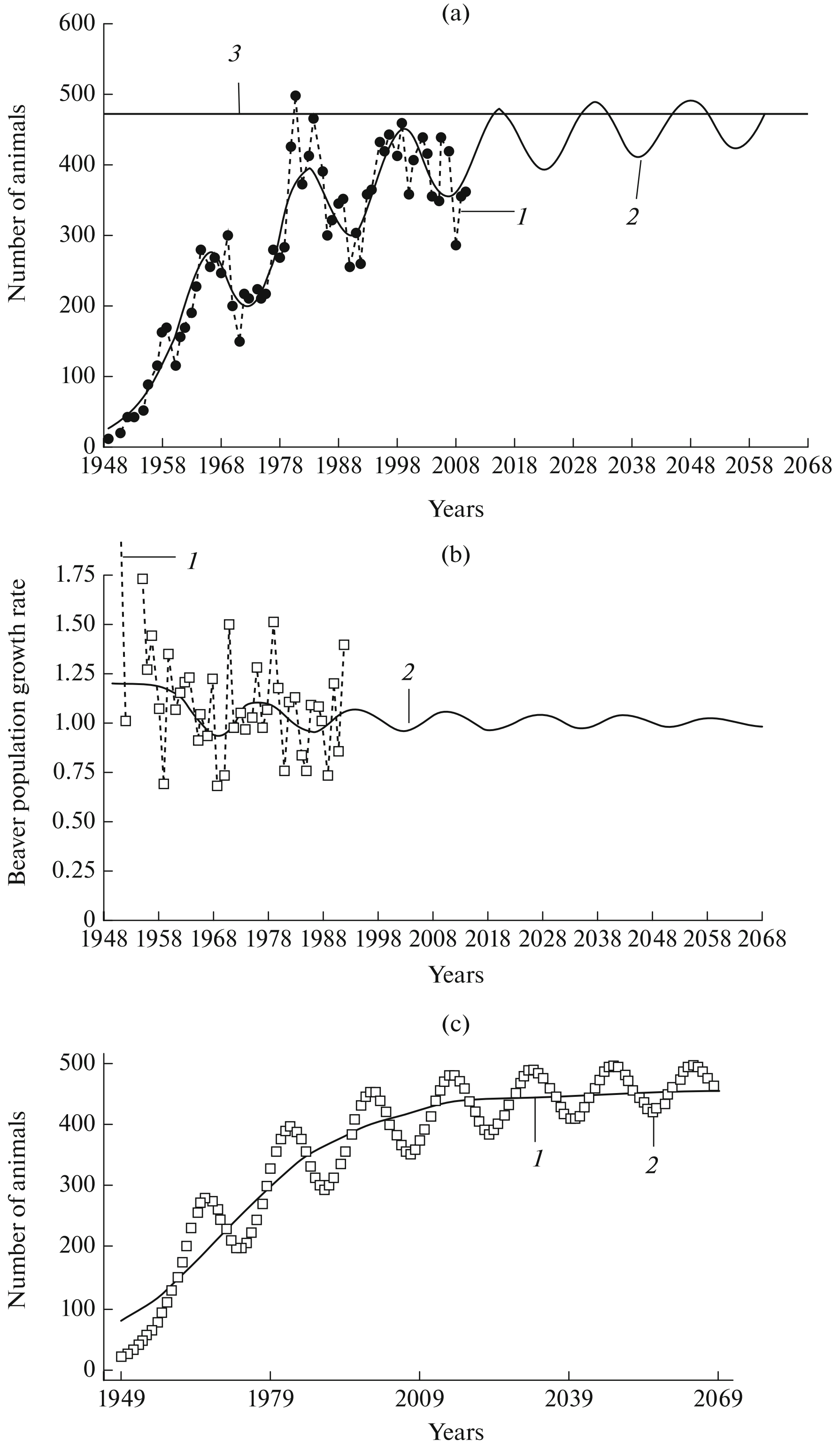

Fig. 6. (a) Beaver population dynamics in the Oksky Reserve (*1*—the survey data; *2*—model estimates; *3*—steady population). (b) Dynamics of the beaver population growth rate (P_{t+1}/P_t) in the Oksky Reserve (*1*—growth rate determined based on the survey data; *2*—its model estimate). (c) Comparison of the logistic and discrete models of beaver population dynamics for the Oksky Reserve (*1*—the curve that describes the logistic trend of population dynamics $\mathrm{P}_{t_k} = 451.763/(1 + \exp(1.62741 - 0.0742073(t_k - 1948)))$; *2*—model estimates obtained using the discrete model).

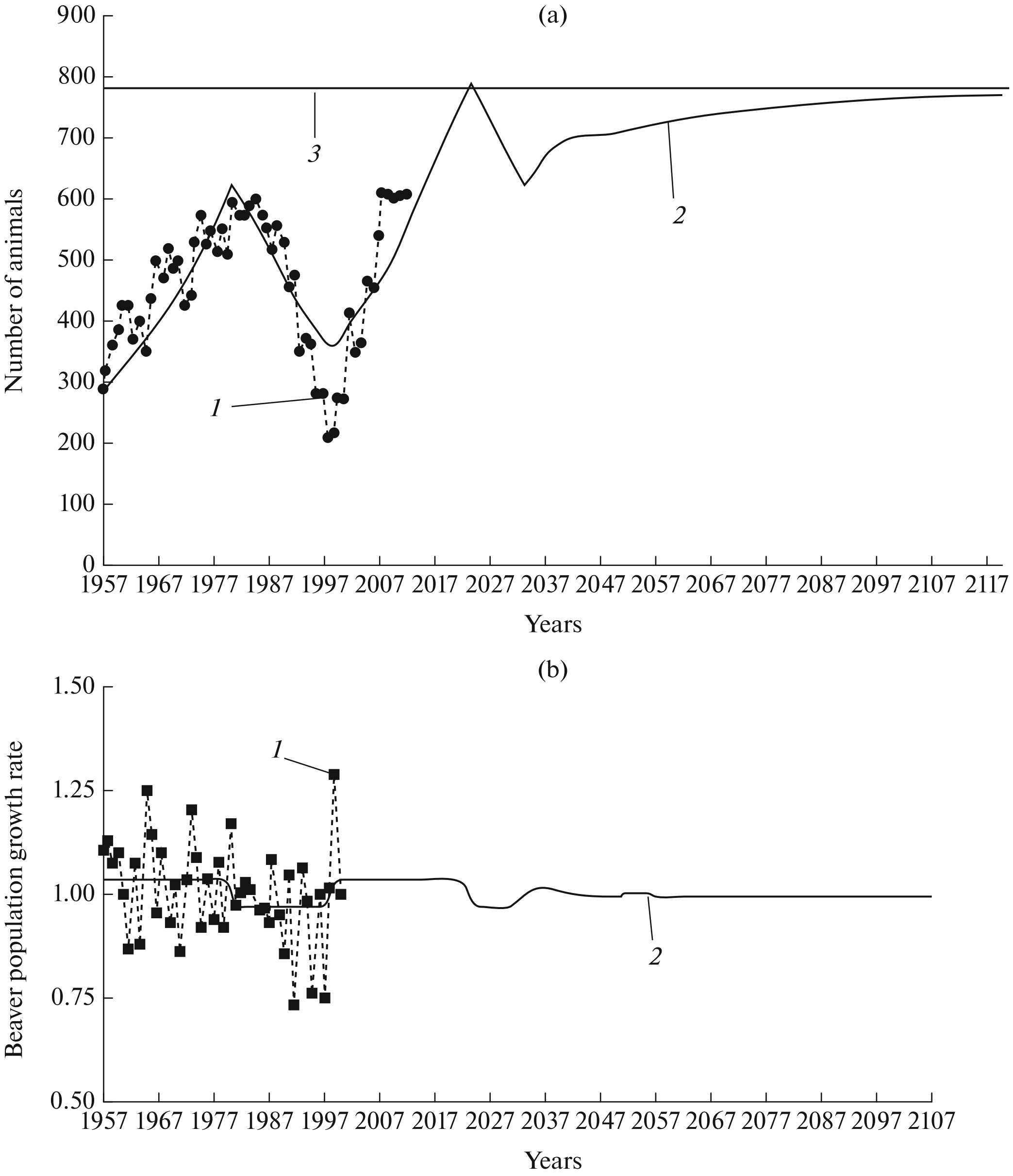

Fig. 7. (a) Beaver population dynamics in the Khopersky Reserve (*1*—the survey data; *2*—model estimates; *3*—steady population). (b) Dynamics of the beaver population growth rate (P_{t+1}/P_t) in the Khopersky Reserve (*1*—growth rate determined based on the survey data; *2*—its model estimate).

We understand the multi-stage pattern as the population dynamics, in case of which the achievement of the first threshold value is followed by the next population growth wave once the necessary conditions are ripe for it. In case of the population dynamics of key species, the multi-stage pattern reflects more complex relationships between animals and their habitats. This pattern is likely to show not only the modern environmental changes due to the activity of key species, but also the accumulated consequences of previous generations, as well as to reflect the greater sensitivity of ecosystems to changes that are made by key species.

In the Lapland Reserve (Fig. 2a), after the reintroduction of beavers in 1934–1937, their population reached the maximum values in 1947–1954. The same years brought about the first signs of the transformation of beaver habitats: the best habitats fell into decay, and the continuous presence of beavers in the same habitat shortened (Kataev, 2011). The beaver population decreased, and in 1970–1980 it was no more than 20 individuals. It is known that the beaver colonies that were established in the vicinity of the reserve were not protected during those years and were gradually extirpated by poachers; whereas the growth in the beaver population in the territory of the reserve was restrained by the slow recovery of woody and shrub food resources. In the Lapland Reserve, the vegetation period is 1.7 times shorter than in Central Russia. The main and almost the only food of the Lapland beavers is birch and willow bark (71 and 27%, respectively). In the Arctic conditions, birch forests recover in beaver habitats so slowly (50–80 years) that the places of beaver feeding were even given a special name in the language of the natives (Kataev, 2011). So, the population size decreased during 1950–1980, and this was due to the absence of virgin uncolonized habitats and slow recovery of food resources in suitable habitats. There is no doubt that young beavers did not manage to find places to form new colonies. Since 1994, the beaver population has been at the consistently low level (see Fig. 2a). If food resources are rather limited, the large beaver population can only survive by reproduction and dispersal (Havens et al., 2013). The latter is not possible in the Lapland Reserve, so the local beaver population is unable to get out of the depression stage. This conclusion is confirmed by new data of Kataev (2015) about the steadily small beaver population in the Lapland Reserve. It is important to note that the analysis of the dynamics in this study was based only on the data for 1934–1985 (Table 1), and the data for a longer period (1934–2009) (Kataev, 2011) was used to assess the accuracy of the prediction. Our additional analysis involving the observations in 1986–2009 showed that the determination coefficient was 0.99, i.e., the discrete model explains the current population dynamics with an accuracy of 99%. It should be noted that the periodic component is completely absent for this reserve (see Table 2). In general, we can state the high quality of the population dynamics prediction for at least 30 years.

Earlier in the literature it was stated repeatedly that the beaver population dynamics is eruptive in most of regions (Teplov, 1960; Kataev and Bragin, 1986; Dvornikova, 1987; Hartman, 1994, 2003; Busher, 2001; Bobretsov et al., 2004). This type of beaver population dynamics was noted in two regions of Sweden: 34 and 25 years after the reintroduction of beavers, the abrupt population growth was replaced by the decline; the population growth rates became negative at densities of 0.25 and 0.20 colonies/km^2, respectively (Hartman, 2003). In other regions, 20–25 years after the beginning of reintroduction and initial population growth, beaver populations decreased and stabilized at the level of 17–23% of the maximum. In the Lapland Reserve, the simulated maximum number of beavers is 108; 18–25 individuals are 17–23% of this population. It can be seen that the upper limit of this interval corresponds (with an error of 4%) to the steady value of 26 individuals (see Table 1). Our analysis that was performed in a wider range of beaver habitats showed that the eruptive population dynamics was observed only if the rate of the recovery of food resources was low, as, for example, in the Lapland Reserve.

According to the results from modeling the beaver population dynamics in the Darvinsky Reserve, the population of beavers grew from 7 to 273 individuals for the first 20 years after their settlement (1980–2000), while in the Lapland Reserve the population increased from 8 to 108 individuals for the first 20 years, i.e., the linear population growth rate was 13.3 individuals/year for the Darvinsky Reserve and 5 individuals/year for the Lapland Reserve. After 1986, the accelerated beaver population growth was observed in the Darvinsky Reserve, since beavers began to colonize the zone flooded by the Rybinsk Reservoir, meliorative channels, ponds, and areas between some big colonies at small rivers. As a result, there were 91 colonies and 273 beaver individuals in the studied region by late 2000 (Zavyalov, 2015). Our model predicts that the first population maximum (about 520 individuals) will be achieved approximately in 2016, after which the next long-term rise to 720 individuals is expected (see Fig. 3a). It is important to note that the next stage of population growth is possible to a significant extent due to the fact that many years of ecosystem-engineering activity of beavers have noticeably improved the conditions for them in the Darvinsky Reserve. The construction of numerous damps has stabilized the hydrological regime of small rivers and streams. The creation of multiple shelters and movement paths (tracks, channels, and “sedge tunnels”) has made it possible for beavers to adapt to life in the changing conditions of the Rybinsk Reservoir and even occupy floating peat islands (Zavyalov et al., 2005; Zavyalov, 2015).

Figures 4a and 4b show that the beaver population dynamics in the Prioksko-Terrasnyi Reserve are characterized by the population’s tending to the steady state in the presence of a quasi-periodic component with periods of 14–26 years. Even before beavers were released into the reserve, it was evident that the Tadenka was not the most favorable habitat; nevertheless, beavers were released there (*Rechnoi bobr*..., 2012). If small groups of beavers are released, the period of population growth to maximal values can be extended up to 40 years even in optimal habitats (Zurowski and Kasperzyk, 1988); so, it is not surprising that on the Tadenka River this period took half a century: from reintroduction in 1948 to the maximum values in 2005. Our analysis shows that the periodic component has a saw-toothed shape; moreover, the beaver population grows from the minimum to the maximum value in each oscillation period for the first 6 years, and then it decreases from the maximum to the minimum value. The amplitudes of quasi-periodic oscillations are about 6 individuals and have a small growth trend. These oscillations may be due to the rate of the recovery of woody and shrub food resources, which have been exhausted in the Tadenka basin by long-term use. For the first colonies, the width of the foraging zone did not exceed 50 m. After multiple habitats recolonizations and in the absence of large predators, the beavers foraging zone extended to 165 m (Goryainova et al., 2014). In general, the type of the beaver population dynamics in the Prioksko-Terrasnyi Reserve can be characterized as single-stage dynamics with a quasi-periodic oscillation.

Figure 5a shows that the beaver population dynamics in the Central-Forest Reserve is complex, which is due to various factors. Beavers were released in small groups (5 and 4 individuals) into the Tyudma River, where the conditions were not initially the most favorable: presence of large predators and low food resources (Yurgenson, I.A. and Yurgenson, P.B., 1951). Another unfavorable factor for beavers was the liquidation of the reserve in 1951–1960 and active poaching at this time. So, while in 1947 there were 62 beavers in all water bodies of the reserve, this number was only 15–16 by 1958. After the restoration of the reserve in 1962, there were only two colonies on the Tyudma River and not more than ten beavers (Solovyov, 1964). Approximately from 1940 to the 1970s, beavers on the Tyudma basin were at the consistently low population level (about five colonies), which corresponded to the maximal capacity of the environment at that time. In 1981–2008, the beaver population was growing in the reserve (Fig. 5a). This was complemented by the accumulation of the results of beavers engineering activity due to a significant growth in the number of colonies in all the Tyudma basin (Zavyalov et al., 2011). In addition, the capacity of the environment significantly increased because of strong windfalls. Large birches and aspens fallen by wind became an additional food source for beavers. Windfall "windows" overgrown with young broad-leaved woody species became main feeding places for beavers in the Tyudma basin. It was catastrophic destruction of mature spruce forests that made it possible for beavers to live in the upper Tyudma. In addition, large windfalls temporarily restricted the movement of large predators. For example, lynxes had a system of regularly used tracks before the windfalls, and after them the animals began avoiding almost insurmountable blockages (Zavyalov et al., 2011). The model predicts that the beaver population will grow from 211 individuals in 2004 to 305 individuals in 2082, and the population of 317 individuals that is steady for the reserve can be reached in a hundred years. According to the model, the Central-Forest Reserve is characterized by the multi-stage beaver population dynamics with a quasi-periodic oscillation.

In the Oksky Reserve (Fig. 6a), 23 beavers that were reintroduced in 1937–1940 found themselves in favorable conditions and began to reproduce intensely. The adaptation to local conditions was primarily manifested in diet changes in accordance with the surrounding vegetation as well as in the construction of various temporary shelters during floods, including special "spring lodges" (Borodina, 1960). Unlike other reserves, there is the logistic population growth with short-period oscillations in the Oksky Reserve (see Fig. 6c). This means that at the initial stage of population development there were no limitations on both vacant habitats and food resources (Pankov and Pankova, 2015). From 1943 to 1953, the beaver population density at the Pra River was low (0.34–0.35 colonies/1 km of the bank line), most of colonies were on oxbow lakes, and the Oka River was not occupied by beavers. From 1954 to 1969, the population density at the Pra River grew up to 0.4–0.6 colonies/km, and the proportions of oxbow and stream colonies became equal; the first colonies appeared in the suboptimal habitats of the Oka River. Since 1960, the population density at the Pra River began to decrease to 0.3–0.1 colonies/km with the subsequent recovery of the density to the former values by 1972. From 1973 to 1990, the colonization of the oxbow lakes of the Pra River slowed down; new colonies appeared in suboptimal habitats of the Oka. At the modern stage of population development (2007–2014), colonization of the oxbow lakes of the Pra River stopped at the population density of 0.66–0.83 colonies/1 km. New colonies appeared on the Oka River, and beavers spending in pessimal habits were observed (Pankov and Pankova, 2015).

The stable growth of the beaver population in the Oksky Reserve and long population existence at a high level were facilitated by the presence of various water bodies, possibilities for young animals to leave their natal territories, and stable food resources. The priorities for different water bodies colonization correlated weakly with the abundance of food resources thanks to large herbaceous and woody food resources on almost all floodplain water bodies of the reserve (Pankov and Pankova, 2015). That is why Kudryashov (1975) came to the conclusion that the intrapopulation mechanisms of population regulation are more important for the beaver population dynamics in the reserve than changes in food abundance. The beavers of the Oksky Reserve have quickly renewable and abundant woody and shrub food resources (osiers). In addition, they intensively feed on macrophytes (*Nuphar lutea, Nymphaea candida, Sparganium erectum, Stratiotes aloides, Scirpus lacustris*), the abundance of which allows for beavers to remain underwater during 2.5–3.5 winter months. At the same time, they make winter food cashes from woody and shrub plants, as well as macrophyte roots (Pankov and Pankova, 2015). On some water bodies of the Oksky Reserve, beavers spend winter continuously, for 50 and more years (Pankova, 2014). All this explains the logistic population growth with a periodic oscillation around the growth trend, which was shown by the model (see Fig. 6c).

After the reintroduction of beavers into Khopersky Reserve, their population began to rapidly grow. Since 1943, beavers began to settle outside the reserve (Zobov, 2005). The colonization of the reserve was in accordance with the general patterns: first, optimal habitats were occupied, followed by suboptimal and pessimal habitats (Zharkov, 1969). In the Khopersky Reserve, floodplain lakes and backwaters of the Khoper River were optimal habitats for beavers.

Therefore, before 1950, beavers mainly occupied these habitats, and only after all of them were occupied beavers began to settle in the channel of the Khoper River and pessimal habitats (marshes and the smallest lakes) (Dyakov, 1975). The colonization of the reserve and achievement of the maximum population density values in the Khopersky Reserve apparently went faster than in the Oksky Reserve. For instance, as early as 1976, out of 154 active colonies, 99 were on floodplain water bodies (64%), while on the Khoper River there were only 55 colonies (36%).

It was reported that when the beaver population reached 400 animals in 1950, the reserve authorities began catch them to introduce beavers into other areas. According to different sources, the number of beavers that were removed from the Khopersky Reserve during the period of 1950–1973 was from 483 (Kuznetsova, 1979), to 616 (Zobov, 2005), to 694 beavers (Chichikin, 1989). Such large numbers were apparently quickly compensated for by the population growth, since beaver numbers and the population density continued to rise. It is worth mentioning that during 1972–1975 the average number of beavers in one colony was 4.2–4.9 animals (Kuznetsova, 1979), i.e., there appeared to be a large number of big colonies with young animals, which could not leave their natal territories for unknown reasons. It is likely that the significant decrease in the beaver population that was observed during the 1980–1990s (Fig. 7a) resulted from the intrapopulation processes of population regulation, which mechanism for beavers was described in detail by Kudryashov (1975) with the Oksky Reserve as an example. It is unclear what role in this population decrease the chages in beaver's food base play. At least, in the 1970s, Kuznetsova (1979) reported the high availability of food for local beavers. According to her observations, beavers did not leave water bodies with degraded woody and shrub vegetation thanks to the abundance of wetland grasses (Kuznetsova, 1979). The beaver population reached its maximum in 1986 (Fig. 7a). The quasi-periodic component of the population dynamics with a 16-year period may be due to two factors: (a) the intrapopulation mechanism when an increasing number of adult non-breeding animals staying with their parents families and not able to leave for the lack of habitats and (b) the periodic reoccurrence of particularly strong (or long) spring floods on the Khoper River, which leads to the "retransformation" of floodplain water bodies (the formation of new water bodies or destruction of old ones).

Generalization of the results of model estimates made it possible to distinguish common characteristics and distinctions of the population dynamics in different reserves depending on systematic and random factors. The proposed conceptual model of the long-term beaver population dynamics has a clear interpretation for different rates of the recovery of food resources in various regions.

If the rate of the recovery of food is low (in the northern periphery of the range, in the Lapland Reserve), the population dynamics is characterized by a short-term irruption with a subsequent decline and trend towards a stable value. This conclusion is confirmed both by the model estimates and by the survey data for 1986–2009 (Kataev, 2011). In the reserve, the small number of animals is explained by beavers intensive foraging on their preferred woody species and very slow recovery of food resources. For example, Kataev (2011) reported that by 1986 the food and protection resources of the Chuna River were exhausted so much that beavers abandoned it and did not settle there for 15 years. This type of dynamics can be considered as the eruptive type (the first type), which was also described in other works (Teplov, 1960; Kataev and Bragin, 1986; Dvornikova, 1987; Hartman, 1994, 2003; Busher, 2001; Bobretsov et al., 2004).

The second type of population dynamics (the single-stage pattern with quasi-periodic oscillations) was observed in the Prioksko-Terrasnyi Reserve. The change in the beaver population is characterized there by the trend towards the steady state with a quasi-periodic component of 14–26 years. Like in other reserves, there it was a gradual accumulation of various beaver objects and their fragments that improve the quality of habitat for beavers, but not so largely as for the reserves with the multi-stage type of population growth. The quasi-periodicity of the dynamics in the Prioksko-Terrasnyi Reserve is due to beavers expanding the foraging zone and their repeated occupation of the earlier used habitats with recovered vegetation (Zavyalov et al., 2016). This type of the dynamics fundamentally differs from the one observed in the Lapland Reserve, where the rate of the recovery of food resources is very low. The Prioksko-Terrasnyi Reserve differs from the Central-Forest Reserve, where the quasi-periodicity of the dynamics is due to large windfalls and significant growth in the capacity of the habitat in proportion to the accumulation of various beaver objects.

If the rate of the recovery of foods is high, long oscillations at the high population level are possible. This type (the third type – the multi-stage pattern with quasi-periodic oscillations) of the animal population dynamics was shown for the Darvinsky, Central-Forest, and Khopersky Reserves. From amongst these three reserves, optimal habitats for beavers existed only in the Khopersky Reserve at the moment of their reintroduction (the abundance of food, shelters, and unoccupied water bodies) (Dyakov, 1975). The habitats of the Darvinsky and Central-Forest Reserves were initially pessimal (strong water level changes at the shore of the Rybinsk Reservoir in the Darvinsky Reserve and a shallow drying-out and freezing river with a small amount of food and abundance of large predators in the Central-Forest Reserve (Zavyalov et al., 2011; Zavyalov, 2015). However, beavers had noticeably changed and improved the living conditions by their long-term ecosystem engineering activity, which was even more favored in the Central-Forest Reserve by windfalls. As a result, the second stage of population growth became possible. The presence of the second stage of population growth in beaver differs from many other alien species, since its population dynamics are largely determined by the strong ecosystem engineering activity and, as a consequence, by the integral growth in the capacity of the environment.

The beaver population dynamics in the Oksky Reserve is characterized by the logistic trend of growth and periodic component of oscillation (16 years) around it (the fourth type). This type is formed in the absence of limitations on the available food resources. From among the series of the studied reserves, it was noted in only one.

The presented four types of dynamics patterns are interpreted well by the proportion of potential resources. This value was 83% for the population dynamics of the eruptive type, 60% for the single-stage type, 36–45% for the multi-stage type, and 28% for the logistic growth.

CONCLUSIONS

The study presented the mathematical model of the beaver population dynamics during many decades, starting from reintroduction, with consideration for the availability and rate of the recovery of resources. The model was implemented for the Lapland, Darvinsky, Prioksko-Terrasnyi, Central-Forest, Oksky, and Khopersky Reserves that are located in European Russia in the north, south, and center of the beaver range. The generalization of the results of the model estimates made it possible to distinguish the common characteristics and distinctions of the population dynamics depending on functional and random factors. Several population development stages were distinguished for the studied reserves. The first two of them characterize the population growth at the first stages of beaver reintroduction. In pessimal habitats, this stage may be lengthened up to 40 years. The implementation of the next stages depends on the rate of the recovery of food resources, accumulation of the results of the ecosystem engineering activity, as well as a number of other factors. The result can also vary: a repeated population growth, logistic growth, and stabilization at the middle and low population level. With all this, oscillation processes are usually superimposed on the curve that reflects the general character of population change (in our analysis, with the exception of one reserve that is located in the northern periphery of the beaver range). The proposed conceptual model of the long-term beaver population dynamics has a clear interpretation for different rates of the recovery of food resources.

At the low rates of recovery and limited amount of available resources, the first type of the eruptive dynamics holds true, i.e., the population dynamics is characterized by a short-term population outburst with a subsequent decline and trend towards a stable steady low value. It was noted in the Lapland Reserve, where the rate of the recovery of woody species harvested by beavers is very low. The second type of population dynamics—the single-stage model with quasi-periodic oscillations—is characterized by tending to the population level that was achieved for the first growth wave in the presence of a quasi-periodic component. It was observed in pessimal habitats of the Prioksko-Terrasnyi Reserve (a shallow river, lack of herbaceous food, and quick exhaustion of woody and shrub food). At the high rate of the recovery of food resources, a significant population growth is possible. This type of population dynamics—the third type: the multi-stage model with quasi-periodic oscillations—was shown for the beaver populations of the Khopersky, Darvinsky, and Central-Forest Reserves. It is important that the possibility of the second population growth wave (the second stage) is related to changes in the capacity of the environment, inclusively, due to the long-term ecosystem engineering activity of beavers that noticeably improves their habitats in these reserves. The fourth type of the dynamics—the logistic population growth up to the high level with a periodic oscillation component—was noted in the Oksky Reserve. It is characterized by the trend towards the steady state in the absence of limitations on the available food resources.

Based on literature data and our own observations, we assume that these four types of the dynamics behavior may also be noted in other parts of the vast beaver range that has formed in the territory of Russia by the present moment.

The performed analysis of the steady solutions has shown that the beaver population dynamics in many reserves is characterized by stability (see Table 1). A stable steady solution and periodic component are completely absent only for the Lapland Reserve. The beaver populations of other five reserves can be divided into two groups. The first group includes the Darvinsky, Oksky, and Khopersky Reserves, for which the steady solutions of the models of beaver population dynamics are stable. For the Prioksko-Terrasnyi and Central-Forest Reserves, the steady solutions are not stable. However, the performed analysis of the dynamics behavior at a fairly long time interval of 1948–2050 and 1936–2136 has shown that variable systems tend to limit periodic functions with time. It follows from here that the model predicts the long-term stable existence of beaver populations under the condition of their natural development.

The performed model study of beaver population dynamics surely has a number of restrictions due to the properties of the territory, course of the invasive process, and possibility of introduction or removal of a part of beavers; however, it gives the quantitative characteristic of the process of beaver recovery in different regions of Russia. Analysis of the long-term beaver population dynamics not only makes it possible to predict the future of beaver populations, but also helps in understanding the direction and scales of the changes in hydrology, soil, plant cover, and animal communities, which can be expected with consideration for the strong transforming activity of beaver.

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