

## Beavers in Russian forest-steppe — characteristics of ponds and their impact on fishes and amphibians

Ivan V. Bashinskiy\* & Vitaliy V. Osipov

**ABSTRACT.** The study of beaver's (*Castor fiber*) impact on steppe rivers' ecosystems was held within the Privolzhskaya Lesostep' State Nature Reserve (Penza Province, Russia). We investigated how pond age and permanence of beaver ponds influenced the abundance and diversity of fishes and amphibians. The majority of beaver ponds in our study area were small and dams were easily destroyed by spring floods. The formation of stable long-term ponds was evident in rivers with low discharge. The most favorable parts of rivers for beavers were anthropogenic reservoirs, where swamping and high biomass of reeds were common. The rivers were inhabited by one species of lamprey (*Eudontomyzon mariae*), six fish species (*Esox lucius*, *Leucaspis delineatus*, *Sabanejewia baltica*, *Misgurnus fossilis*, *Barbatula barbatula*, *Carassius carassius*), and five amphibian species (*Lissotriton vulgaris*, *Pelobates fuscus*, *Bufo viridis*, *Rana arvalis*, *Pelophylax lessonae*). As a result of the damming, abundance, biomass of fishes, species diversity and abundance of amphibians increased. During long-term persistence of beaver ponds fish abundance declined (the oxygen level reduced), but the number of amphibians continued to appear (more shallow water bodies appeared). Also beaver dams led to isolation of fishes in different parts of valleys and served as barriers to spawning migrations (e.g. for pike and lamprey). When beavers abandoned ponds, amphibian abundance declined, and fish abundance increased — due to increased water flow. Thus, despite some positive effects, beaver ponds were not the key habitats for fishes and amphibians.

**KEY WORDS:** *Castor fiber*, impact on ecosystems, fishes, amphibians, small rivers, forest-steppe.

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## Бобры в лесостепной зоне России: особенности прудов и их воздействие на рыб и амфибий

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**РЕЗЮМЕ.** Было проведено исследование воздействия бобра (*Castor fiber*) на экосистемы лесостепных рек в окрестностях заповедника «Приволжская лесостепь» (Пензенская область, Россия). Было показано, как возраст и стабильность бобровых прудов влияют на обилие и видовое разнообразие рыб и амфибий. Большинство бобровых прудов имеет небольшие размеры, плотины ежегодно размываются. Образование стабильных многолетних прудов было возможно на реках с небольшим расходом воды. Наиболее крупные поселения образовывались на месте старых антропогенных водоёмов, где сохранилось остаточное заболачивание и наблюдается высокая биомасса травянистой растительности. Бобровые реки в степи заселены 7 видами рыб и рыбообразных (*Eudontomyzon mariae*, *Esox lucius*, *Leucaspis delineatus*, *Sabanejewia baltica*, *Misgurnus fossilis*, *Barbatula barbatula*, *Carassius carassius*) и пятью видами амфибий (*Lissotriton vulgaris*, *Pelobates fuscus*, *Bufo viridis*, *Rana arvalis*, *Pelophylax lessonae*). В результате запруживания водоёмов обилие и биомасса рыб возрастает, так же, как и видовое разнообразие и обилие амфибий. В процессе продолжительного существования прудов численность рыб уменьшается (вследствие снижения уровня растворенного в воде кислорода), а численность амфибий увеличивается (благодаря увеличению площади мелководий). Помимо этого, бобровые плотины приводят к физической изоляции рыб на разных участках рек и служат барьером для нерестовых миграций некоторых видов (украинская минога, щука). Когда бобры покидают пруд, численность амфибий снижается, а численность рыб увеличивается — благодаря появлению большей проточности. Несмотря на некоторое положительное влияние, бобровые пруды в условиях лесостепи Европейской части России не являются ключевыми местообитаниями для рыб и амфибий.

**КЛЮЧЕВЫЕ СЛОВА:** *Castor fiber*, воздействие на экосистемы, рыбы, амфибии, малые реки, лесостепь.

## Introduction

Expansion of beaver population in Russia and ecosystem changes due to climate and anthropogenic processes caused a lack of adequate habitat for beaver relative to food resources, suitable geomorphology and hydrological conditions; therefore, they occupied unsuitable territories. This form of habitat selection is evident in steppe and forest-steppe regions of the Penza Province in south part of central Russia.

Increasingly, novel investigations of beaver's impact on ecosystems are a developing field of ecology science. But just few countries had studies about that topic, e.g. Canada, USA, Germany, Lithuania (Naiman *et al.*, 1988; Nummi, 1989; Balciauskas *et al.*, 2001; Halley & Lamberg, 2001; Dalbeck *et al.*, 2007; Parker *et al.*, 2007; Parker & Rønning, 2007; Dalbeck & Weinberg, 2009; Hill & Duval, 2009). The majority of research about beaver's influence concerns North American populations of *Castor canadensis* (Baker & Hill, 2003; Gallant *et al.*, 2004; Westbrook *et al.*, 2006; Hood & Bayley, 2008; Karraker & Gibbs, 2009; Hood & Larson, 2014; Anderson *et al.*, 2015). In Russia, due to reporting systems within protected areas and unpublished scientific information kept in nature reserves, there is opportunity for extensive and complex researches regarding a broad range of beaver-modified ecosystems (Zavyalov *et al.*, 2005; Krylov & Bobrov, 2007; Osipov, 2011; Dgebuadze *et al.*, 2012; Bashinskiy, 2014).

Previous studies took place in forest ecosystems; therefore, forest-steppe rivers have not yet been subject to the assessment of ecological role of beavers. Features of biotic and abiotic processes as well as age of beaver populations and settlements, relief and hydrological characteristics differ in different ecosystems over time. So that results in differences of beaver impact on various territories (Zavyalov *et al.*, 2010; Dgebuadze *et al.*, 2012) and for understanding of beavers' role it's necessary to study territories with other conditions.

Our main research goal was to develop a preliminary classification of beaver habitats in forest-steppe river ecosystems to assess the primary ways that beavers impact on fishes and amphibians. Our objectives were to:

- classify the most common beaver habitats of forest-steppe rivers.
- quantify fish populations of beaver rivers relative to species diversity, abundance.
- quantify amphibian populations – species diversity, abundance.
- identify differences between the ecosystems-specific impacts of beaver rivers in forest and forest-steppe rivers.

## Material and methods

Our study was conducted in Penza Province, located in the central part of forest-steppe region of Russia (Fig. 1) in 2014–2015. It is typical forest-steppe region,

with half of its territory occupied by mixed-wood forest and the southern part by grassland. There is state nature reserve within the Penza Province, it consists of five parts, three of which with forest-steppe and steppe landscapes. There are four small rivers within forest-steppe parts of the reserve, which comprised our study sites. Our primary research area was in the Ostrovts-ovskaya Lesostep', which contains a permanent and well-developed river network with a high diversity of habitats. Within the reserve other streams were temporary, but all of them were inhabited by beavers.

During our study, some typical parts of river valleys were chosen randomly and described with following parameters — size of beaver ponds, water depth, flow rate (if present), temperature of water, amount of dissolved oxygen (with Hanna Instruments Dissolved Oxygen Meter HI-9142), pH (with Hanna Instruments Portable pH/ORP/EC/Temp “Water Test” Meter HI 98204), lighting (with lux-meter Testo 540) and main vegetation. We used a Garmin 60Cx handheld GPS unit to map all beaver dams and perimeters and outlines of ponds (error  $\pm$  3 to 5 m).

For ichthyologic research, we used several types of traps to accommodate different species and different habitats, lift-nets (1×1 m), nets, funnel traps (nine traps over 34 days) and electrofishing (DEKA 3000). For each sampling site, we used the same set of traps for the same trapping duration. We also surveyed 10 m<sup>2</sup> of each habitat adjacent to the traps to quantify the abundance and biomass of fishes. We then standardized these values by habitat area and catching effort. Six hundred ten (610) fish individuals were caught and measured or otherwise categorized (i.e. body length, weight, sex, age).

For our amphibian research we conducted visual surveys, trail censuses, dip-net sampling (Heyer *et al.*, 1994; Skelly & Richardson, 2010), drift fences with buckets (21 ten-meter fences over 38 days). Drift-fences were established around three beaver ponds, with ten-meter intervals (*sensu* Yermokhin & Tabachishin, 2011) to allow for the incomplete enclosure of water body.

Besides habitats on small rivers of the reserve, there were some other natural water objects inhabited by beavers — the nearby the Khoper River and its oxbows. They were chosen as control habitats because they were the natural refugees of fishes (Khoper) and amphibians (oxbows) for small rivers and new beaver habitats. We repeated our surveys four times during the spring and summer.

For statistical analysis we used software programs Statistica 7.0 and Microsoft Office Excel 2007. Correlations were tested with Spearman's rank correlation coefficients.

## Results and discussion

**Habitats.** We compiled detailed descriptions of four small rivers flowing through the three parts of the Privolzhskaya Lesostep' Nature Reserve (Tab. 1). We focused on the Selimutka River and its tributary the

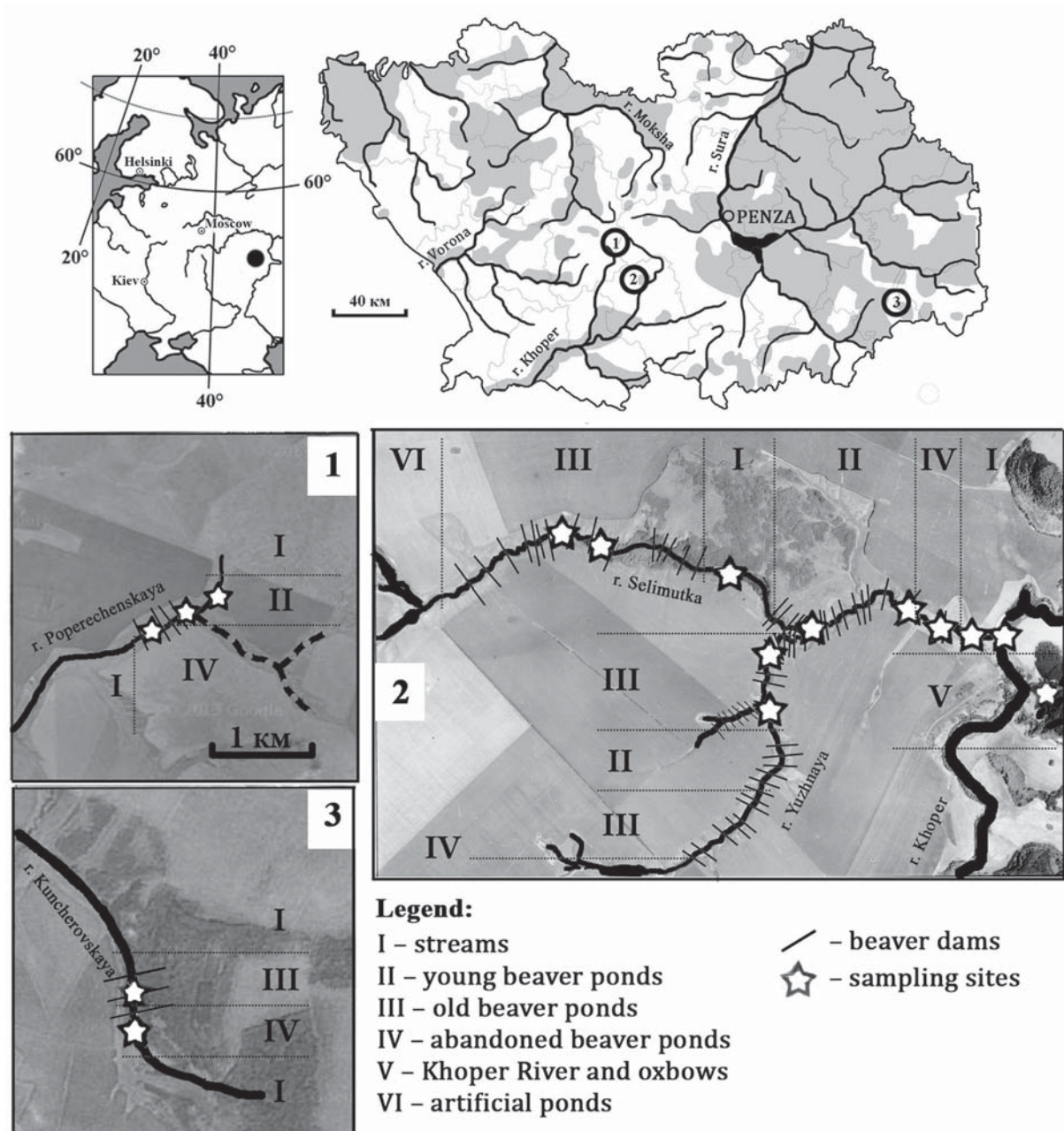


Figure 1. Study area and main types of habitats where investigations of beaver impact on fishes and amphibians were held in 2014–2015. Areas within the Privolzhskaya Lesostep' Nature Reserve (Penza Province): 1 — Poperechenskaya Step'; 2 — Ostrovtsovskaya Lesostep'; 3 — Kuncherovskaya Lesostep'.

Yuzhnaya River within the valley of the Khoper River, because it represented the most advanced and constant river system and had a variety of habitats (Fig. 1). We then divided the beaver habitats within these rivers into four types depending on the degree of the impact of beavers — streams without beaver activities, young beaver ponds, old beaver ponds and abandoned beaver ponds.

*Streams without beaver activities.* Beavers used these rivers only during dispersal for migrations and do not construct dams in these locations. According to our

observations the main reasons for absence of beavers in some reaches of the forest-steppe rivers were lack of food resources due to sparse woody deciduous vegetation, steep slopes caused by erosion typical of the forest-steppe zone, and some anthropogenic factors (agriculture, hunting). These streams can have both high flow rates (0.37 m/s — lower part of Selimutka River) and relatively slow flow rates (0.05 m/s — Yuzhnaya River). Typically, streams were characterized by lower water temperatures and increased levels

Table 1. Characteristics of four small rivers inhabited by beavers in the Privolzhskaya Lesostep' Nature Reserve, Russia, spring–summer of 2014–2015.

	Poperechenskaya Step'	Ostrovtsovskaya Lesostep'		Kuncherovskaya Lesostep'
Small river	Poperechenskaya River	Selimutka River	Yuzhnaya River	Kuncherovskaya River
Year when beavers appeared	2012	2004	2004	2011
Dams per 1 km of river	less than 3	3.7	6.4	less than 3
Water discharge, m <sup>3</sup> /s	0.003	0.1–0.17	0.001	0.001

Table 2. Characteristics of the main types of habitats inhabited by beavers in the Privolzhskaya Lesostep' Nature Reserve, Russia, spring–summer of 2014–2015. Maximum values are in bold and minimum values are in italics, mean values are below.

Type of habitat	Area (m <sup>2</sup> )	Depth (m)	Amount of dissolved oxygen, (mg/L)	pH	Lighting (1000s lux)	Temperature of water, (°C)
Streams	30–100	<i>0.05</i> –0.3	3.5– <b>11.5</b>	7.2–8.1	3.8–41	<i>10.1</i> –21.5
	46	0.15	7.12	7.9	22.4	16.8
Young beaver ponds	90–3000	0.4–0.8	2.5–9.4	7.7–8.1	7.6–56	10.9–20.8
	1110	0.43	8.6	7.9	29.22	19.46
Old beaver ponds	400– <b>8250</b>	<b>0.3</b> – <b>1.5</b>	<i>0.5</i> –11.2	<i>7.4</i> –8.2	7.8– <b>75</b>	14.5–21.5
	1878.13	0.56	6.66	7.75	37.96	18.89
Abandoned beaver ponds	25–1936	0.1–0.5	3.9–11.2	<b>7.8</b> – <b>8.5</b>	5.6–56	12.1– <b>29</b>
	980.5	0.13	7.73	8.3	24.87	24.33

of dissolved oxygen (Tab. 2). Nearby vegetation usually was represented by *Alnus glutinosa*, *Urtica dioica*, *Butomus umbellatus*, *Filipendula ulmaria*, *Carex pseudocyperus*, *C. acuta*, *C. vesicaria*, *Sagittaria sagittifolia*, *Epilobium palustre*, *Rumex hydrolapathum*.

**Young beaver ponds.** Ponds that were formed in the past one to two years, or had narrow “riverbed” topography and high floods events, washed away the dam each year. Such habitats often had lower food resources, which resulted in rapid abandonment by beavers (in 1–2 years). The area of the ponds ranged from 90 to 3000 m<sup>2</sup>, with a mean about 1100 m<sup>2</sup> depth about 0.4 m (Tab. 2). Vegetation was represented by *Alnus glutinosa*, *Carex acuta*, *C. riparia*, *C. vulpine*, *Lythrum salicaria*, *Bidens cernua*, *Sparganium erectum*. After damming and the creation of the beaver pond, more water plants appeared (e.g. *Lemna minor*, *Lemna trisulca*, *Elodea canadensis*, *Ceratophyllum demersum*, *Glyceria fluitans*).

**Old beaver ponds.** Old beaver ponds were considered to be any pond greater than three years old. They were usually located on streams with low discharge, so beavers should build cascades of dams. Old ponds reached large sizes, with areas up to 8000 m<sup>2</sup> with a maximum depth up to 1.5 m (Tab. 2). The lowest oxygen level was found in old beaver ponds. These

characteristics could be because the largest beaver ponds were situated on sites of former artificial reservoirs. So some relief changes, water logging and man-made elements (e.g. dams, road embankments) might have helped beavers maintain water levels and also provided them with large plant biomass (e.g. willows, reeds). Willows and emergent plants were common vegetation types in the study area (e.g. *Phragmites australis*, *Carex acuta*, *C. pseudocyperus*, *C. vesicaria*, *Lemna minor*, *L. trisulca*, *Bidens cernua*, *B. tripartite*, *Filipendula ulmaria*, *Urtica dioica*, *Persicaria amphibian*, *Sagittaria sagittifolia*, *Lysimachia vulgaris*, *Scirpus lacustris*).

**Abandoned beaver ponds.** Abandoned ponds appeared after the destruction of dams by floods or human activities. They differed from streams because of elements of beaver activities: remains of dams, beaver channels, shallow waters, and more lighting due to loss of some trees. Flow rates and depths decreased after water impoundment by beavers. Vegetation was similar to the vegetation of streams, but had fewer trees because of cutting and forage activities of beavers. If destruction of ponds occurred in the spring and summer, availability of herbaceous vegetation could be lower in the fall. Usually, after a year, if there was no recolonization by beavers, these areas of the river returned to original state.

Table 3. Fishes of the small rivers inhabited by beavers in the Privolzhskaya Lesostep' Nature Reserve, Russia, spring–summer of 2014–2015. S — Selimutka River, Yu — Yuzhnaya River, Kh — Khoper River.

Species	River		
	S	Yu	Kh
<i>Leucaspis delineatus</i>	+++	+++	+
<i>Carassius carassius</i>	–	+	–
<i>Carassius auratus</i>	–	++	–
<i>Tinca tinca</i>	–	+	–
<i>Rutilus rutilus</i>	–	–	+++
<i>Alburnus alburnus</i>	–	–	+
<i>Rhodeus sericeus</i>	–	–	++
<i>Gobio gobio</i>	–	–	+
<i>Leuciscus cephalus</i>	–	–	+
<i>Barbatula barbatula</i>	++	+	+
<i>Sabanejewia baltica</i>	+	–	+
<i>Cobitis taenia</i>	+	–	+
<i>Eudontomyzon mariae</i>	+	–	+
<i>Misgurnus fossilis</i>	+	+	–
<i>Esox lucius</i>	+	+	+

Note: +++ abundance of species more than 50% of all fishes caught, ++ abundance of species 10–49%, + abundance of species less than 10%, – species was not caught.

**Fish populations.** We found 14 species of fishes and one species of lamprey in the study area (Tab. 3). The highest number of fish species ( $n = 11$ ) was observed in the control habitat (i.e. the Khoper River). Large size of the river and high flow rates prevented extensive beaver activities in the river; therefore, fish fauna of the river had a high diversity and large numbers of riverine species (e.g. *Rutilus rutilus*, *Gobio gobio*, *Leuciscus cephalus*), which were not found in the small rivers, inhabited by beaver. In such habitats maximum species diversity was found in streams part of the Selimutka River (from four to seven species). By abundance, the dominant species of fishes were *Barbatula barbatula* and *Leucaspis delineatus* (Fig. 2), and by biomass, the dominant species was lamprey *Eudontomyzon mariae*. However, lampreys were only found in habitats located below all dams. In the same parts of the river, *Sabanejewia baltica* were found, although it was not found in other habitats. Streams in the central section of river, between beaver dams, were solely inhabited by *Barbatula barbatula*. This species was found in all types of beaver habitats of the rivers, with the highest abundance in undammed areas. Another species found throughout the river was *Misgurnus fossilis*. Due to the different requirements of fish species relative to environmental conditions their distribution differed (Fig. 2). *Misgurnus fossilis* can breathe

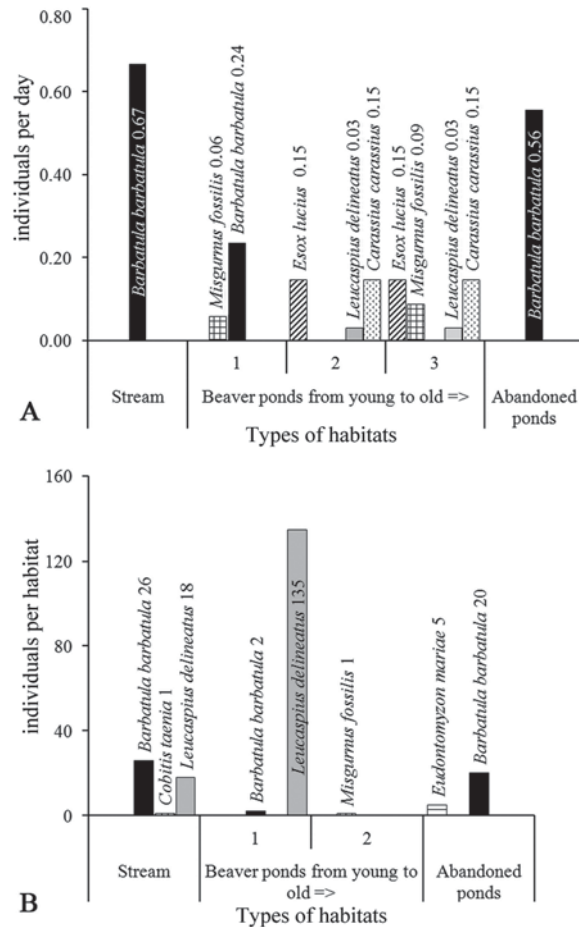


Figure 2. Abundance of fishes in different types of beaver habitats of the Privolzhskaya Lesostep' Nature Reserve (Penza Province), spring–summer 2014–2015: A — data from funnel traps, individuals per day; B — data from electrofishing, total amount of individuals per habitat.

atmospheric air; therefore, it can live even in old ponds with lack of dissolved oxygen (Reshetnikov, 2003). Also, pike (*Esox lucius*) were found in all types of habitat; it annually went up from river mouth to upper parts for spawning and after that returned downstream. However, sometimes adults and yearlings were trapped in ponds until the next high flood event. In young beaver ponds, we caught only two species (Fig. 2), and in old beaver ponds, we caught four species. In comparison with other habitats, *Barbatula barbatula* usually disappeared from ponds due to low oxygen level.

The biomass of fishes in rivers increased after beavers dammed streams, although measures differed by sampling method as well (Fig. 3). In beaver impoundments minimum biomass was observed at the youngest (1-year-old) and the oldest (more than 3-year-old) ponds. The highest biomass in young ponds was formed by *Leucaspis delineatus*, in old ponds by *Misgurnus fossilis*, *Esox lucius* and *Carassius carassius*. Mean biomass decreased and reached a minimum when beavers abandoned the pond and pond was destroyed, although

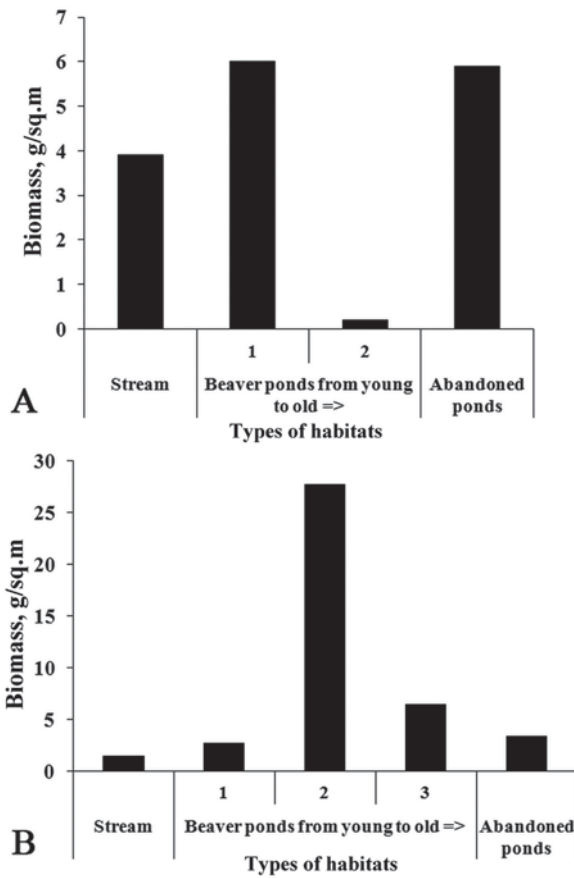


Figure 3. Biomass of fishes in different types of beaver habitats of the Privolzhskaya Lesostep' Nature Reserve (Penza Province), spring–summer 2014–2015: A — data from funnel traps; B — data from electrofishing.

these sites retained higher biomass values than those in undammed streams.

The distribution of fishes was associated with dissolved oxygen, but correlation was weak ( $r=-0.29$ ,  $p < 0.05$ ) (Fig. 4). Dissolved oxygen was also associated with the presence of beavers ( $r=-0.74$ ,  $p < 0.05$ ). However, fish fauna in these rivers was mainly limnophilic; therefore, oxygen could not be a limiting factor. The more important factor influencing fish distribution in rivers of the forest-steppe was their physical isolation, which we observed in different parts of small river valleys. In the spring we saw about ten lampreys spawning near the lowest dam where they could not pass. The absence of lamprey in the higher parts of river flow suggests that beaver ponds could affect the life cycle of the species that listed in the Red Data Book of the Russian Federation (The Red Data Book..., 2001). It is also possible that beaver dams might serve as a barrier for other species of fishes. Isolation occurred also in upper parts of river valleys. Anthropogenic pond, located in upper part the Yuzhnaya River, was inhabited by two fish species (*Carassius auratis*, *Tinca tinca*), which were not found in lower parts of river, so we could assume that dams were barriers for these fishes. Periods of weak spring floods and isolation due to low water level also affected pike, although that fishes could access the majority of habitats during the spring flood.

**Amphibians.** We found seven species of amphibians, five in the valleys of small rivers and two species exclusively in the control habitat (Tab. 4). All species spawned only in beaver ponds within river valley; streams are not suitable because these species require standing water for breeding (Kuzmin, 2012). Streams without beaver were used by two species of frogs (*Rana arvalis* and *Pelophylax lessonae*) exclusively during dispersal.

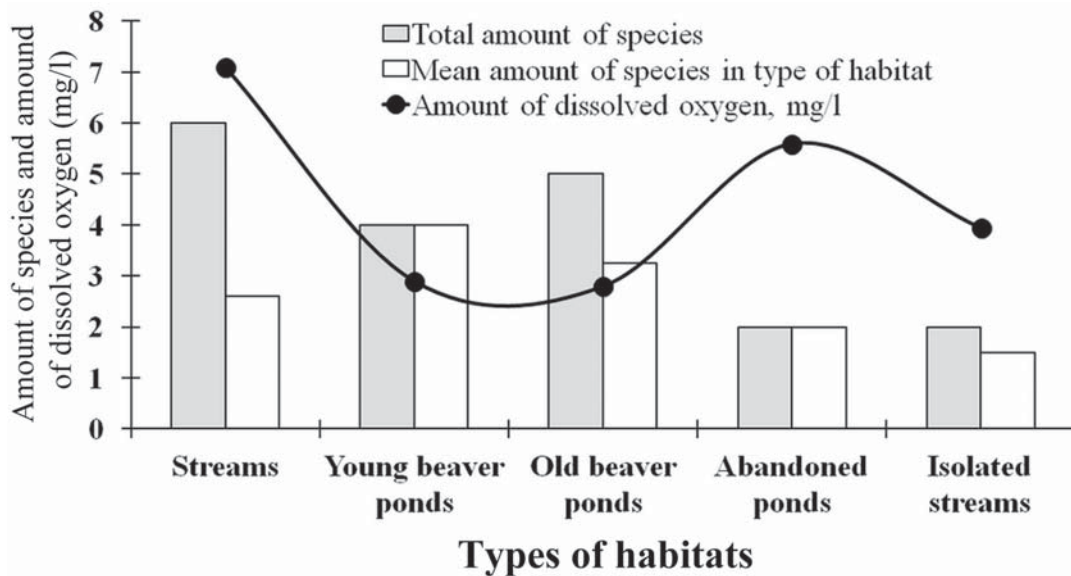


Figure 4. Number of fish species and amount of dissolved oxygen in different types of beaver habitats of the Privolzhskaya Lesostep' Nature Reserve (Penza Province), spring–summer 2014–2015.

Table 4. Distribution of amphibians in different habitats inhabited by beavers in the Privolzhskaya Lesostep' Nature Reserve, Russia, spring–summer 2014–2015. Parts of the nature reserve include: P — Poperechenskaya, O — Ostrovtsovskaya, K — Kuncherovskaya.

Species	Stream			Young beaver ponds		Old beaver ponds			Abandoned beaver ponds			Oxbow (control)
	P	O	K	P	O	P	O	K	P	O	K	O
<i>Lissotriton vulgaris</i>	–	–	–	–	–	–	+	–	–	–	–	+
<i>Triturus cristatus</i>	–	–	–	–	–	–	–	–	–	–	–	+
<i>Bombina bombina</i>	–	–	–	–	–	–	–	–	–	–	–	+
<i>Pelobates fuscus</i>	–	–	–	+	–	–	+	+	–	–	–	+
<i>Bufo viridis</i>	–	–	–	–	–	+	–	–	+	–	–	–
<i>Rana arvalis</i>	*	*	*	+	+	+	+	+	+	*	*	+
<i>Pelophylax lessonae</i>	*	*	*	+	*	+	+	+	+	*	*	+

Note: \* species was present but did not spawned, + species was present and spawned, – species was absent.

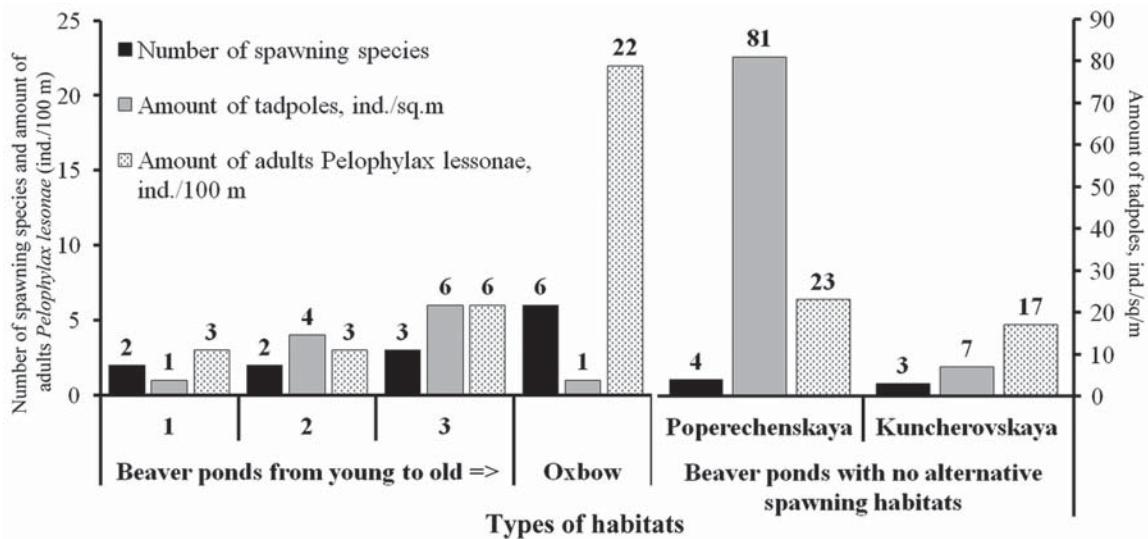


Figure 5. Characteristics of amphibian population in different types of beaver habitats of the Privolzhskaya Lesostep' Nature Reserve (Penza Province), spring–summer 2014–2015: A — Ostrovtsovskaya Lesostep'; B — Poperechenskaya Step' and Kuncherovskaya Lesostep'.

The highest species richness and abundance was in the old beaver ponds, which contained more shallow water and flooded meadows (Fig. 5). The youngest ponds usually were located in unsuitable habitats for beavers and were washed-out by floods annually. Therefore, spawning by amphibians was rare in these habitats, although sometimes small shallows were used by ubiquitous species (*Rana arvalis*).

However, when comparing the data of amphibian population of river valleys with the control habitat, the maximum abundance and number of species was in large oxbows (Fig. 5). These water-bodies were selected more often by amphibians because they were more stable than younger beaver ponds, and old beaver ponds were formed too far (1.5–2 km) from traditional breeding sites. The greatest differences between oxbows and

beaver ponds could be seen with abundance of juveniles that left the ponds after metamorphosis (Fig. 6). There was a low degree of reproductive success for amphibians in old beaver ponds. Despite the number of tadpoles was similar in old ponds and oxbows (Fig. 5), number of juveniles differed a lot in these habitats (Fig. 6). However, the number of adults of *Pelobates fuscus* and *Rana arvalis* near the old ponds was higher than those near the oxbow lake. That fact concerned not benefits but lack of suitable habitats. Oxbows were situated in the forest and surrounded by other flood-plain water-bodies, while the old ponds on forest-steppe rivers were surrounded by open landscape so terrestrial amphibians stayed close to ponds.

These findings were valid primarily for valley of the Selimutka River, but on streams located far from stand-

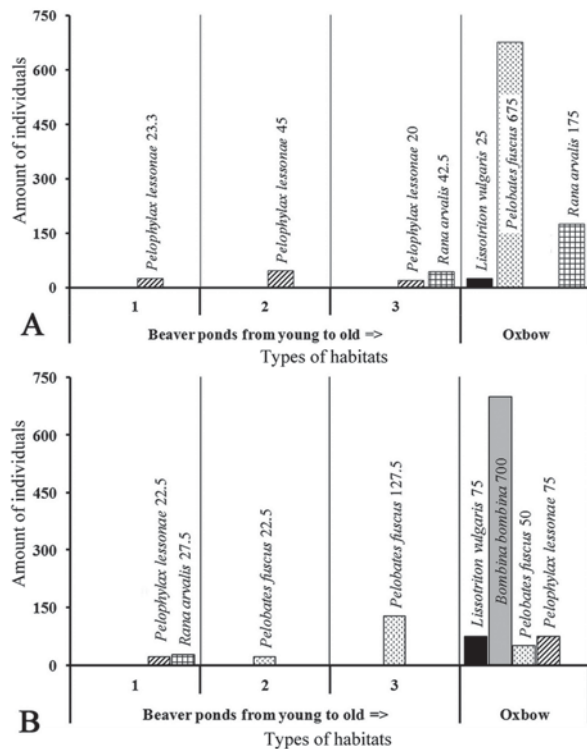


Figure 6. Abundance of amphibians in beaver ponds and in the control habitat (oxbow) of the Privolzhskaya Lesostep' Nature Reserve Nature Reserve (Penza Province), summer 2015: A — juveniles, B — adults; total amount of individuals for all study period (38 days).

ing water (e.g. Poperechenskaya and Kuncherovskaya rivers) beaver ponds provided the only suitable habitats for amphibians. Abundance and species richness of amphibians on such rivers exceeds the data from Selimutka valley area, where oxbows were alternative natural spawning sites (Fig. 5). But because these ponds were inhabited by small families of beavers or young individual beavers due to a shortage in food, the loss of beavers might have resulted in a corresponding absence of amphibians.

## Conclusion

In the forest-steppe zone of south part of central Russia, the impact of beaver was similar to its influence in forests, but there were some differences. Due to the geomorphological and hydrological characteristics of the region, the formation of large beaver impoundments was possible in small streams with low water flow; other rivers were usually populated by small families or young individuals. In these areas beaver ponds were narrow, unstable, and dams were destroyed annually because of spring floods. Abandoned ponds in rivers of the forest-steppe generally were similar to undammed streams, despite some siltation, shallow waters and flooded meadows that remained following abandonment by beavers. This was one of the most important

differences from a forest zone where abandoned beaver ponds were often unique habitats, which could be very important for valley ecosystems (Bashinskiy, 2014).

Distribution of fish population of rivers in the forest-steppe was determined by two main factors: the type of beaver habitats (e.g. by age or location) and physical isolation by beavers. Thus, the highest species diversity of fishes was found in undammed streams, and the lowest in young beaver ponds. Beaver ponds were characterized by the highest fish biomass. Streams below all beaver settlements were inhabited by fishes more readily, because fishes could access them from the river mouth. In addition, beaver dams had negative impact on life cycles and spawning migrations of lamprey and some fish species.

The impact of beavers on amphibians was most important on small streams and in areas where other suitable water bodies lacked beaver ponds. In other areas, the benefits of the damming of the small rivers resulted in the most common and the most abundant species (e.g. *Pelobates fuscus*, *Rana arvalis*, *Pelophylax lessonae*).

Some of the beaver ponds were formed in areas that formerly consisted of artificial ponds. As such, the new beaver ponds replaced these artificial structures. It might be especially important within nature reserves, where anthropogenic interference with ecosystem processes is less common. For the forest-steppe region, there is typically a lack of natural lakes; therefore, the main larger lentic waterbodies with consist of artificial reservoirs (Ivushkin *et al.*, 2001). At the same time there is dense river system and most streams are small rivers that are actively populated by beavers. Therefore we find two processes: 1) large numbers of beaver ponds on the slow-moving streams, and 2) artificial reservoirs degraded due to socio-economic reasons. These reservoirs are maintained for human uses (agriculture, recreation) and are unsuitable for many taxa; therefore, beaver ponds could become an alternative to artificial ponds for the conservation of aquatic ecosystems.

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