REVIEW PAPER

The Eurasian Beaver (*Castor fiber*) as a Keystone Species – a Literature Review

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Abstract

The Eurasian beaver (*Castor fiber*) is a keystone species that has a disproportionately large effect on ecosystem structure and function relative to its abundance and biomass. The variety of roles played by beavers in the ecosystem has been extensively discussed in the literature, and certain aspects of beaver activity have been explored in greater depth than others. The aim of this study was to summarize publications that analyze the impact of beaver habitats on changes in the quality and quantity of local fauna.

Key words: Eurasian beaver, *Castor fiber*, impact, biodiversity

Introduction

The Eurasian beaver (*Castor fiber*) is a keystone species that has a disproportionately large effect on ecosystem structure and function relative to its abundance and biomass (Jones et al. 1994, Paine 1995). In nature, animals generally adapt to the existing habitats but the same cannot be said of beavers. Beavers transform watercourses and the banks of water bodies to exploit selected natural resources for their life needs. The habitats created, transformed and preserved by beavers support the development of plants and other animals (Hartman and Axelsson 2004, Törnblom et al. 2011, Ulevičius and Balčiauskas 1999). Beavers actively modify their habitats by building dams, lodges, canals and digging dens along river banks where they nest and store food. Beavers have highly unique and selective foraging preferences that considerably influence the habitats colonized by the species. The effects of their foraging activities are particularly visible in fall and winter, when the animals cut down trees and shrubs in the vicinity of rivers and water bodies (Belova 2006, Dvořák 2013, Dzięciołowski and Misiukiewicz 2002, Janiszewski et al. 2006, Margaletic et al. 2006).

The most characteristic and creative manifestation of beaver engineering activities are dams that are built across watercourses to slow down water flow and raise water levels. Dams lead to flooding and the formation of large areas that retain water. In ponds that are formed along watercourses and streams, beavers maintain the water table at an appropriate level to ensure that entrances to lodges are always submerged, which enables the animals to travel safely between the pond and the coastal zone (Żurowski 1992).

The variety of roles played by beavers in the ecosystem have been extensively discussed in the literature, and certain aspects of beaver activity have been explored in greater depth than others. Beavers are involved in the following types of activities that transform their natural habitats (Collen and Gibson 2001, Dyck and MacArthur 1993, Fyodorov and Yakimova 2012, Fustec and Cormier 2007, Woo and Waddington 1990):

1. Storage of rainwater that is gradually released during periods of drought;
2. Slowing down river flows;
3. Flooding areas adjacent to beaver ponds and canals;
4. Equalizing water levels;

5. Increasing the area of open spaces (not canopied by trees) in forests;

6. Decreasing the populations of wild animals that graze on dicotyledonous trees in coastal zones;

7. Improving or degrading fish habitat conditions;

8. Improving habitat conditions for animals those live at the bottom of ponds and in areas surrounding ponds, dead trees and other aquatic environments with limited water flow;

9. Replacing invertebrates that inhabit flowing waters with species that thrive in bodies of standing water;

10. Increasing insect biomass;

11. Increasing plankton biomass;

12. Intensifying sedimentation and decreasing water turbidity in deeper strata of watercourses;

13. Creating supportive conditions for the growth of selected tree species, including willows and alders;

14. Increasing the concentrations of organic carbon, nitrogen (and nitrogen availability) and other elements in beaver canals;

15. Intensifying the decomposition of nitrogen compounds by microorganisms colonizing bottom sediments, promoting carbon circulation;

16. Improving the pH of stream water;

17. Increasing organic matter levels for methane-producing bacteria and increasing the concentrations of carbon produced during methanogenesis;

18. Reducing the oxygen content of water in spring and early summer by decomposing rich deposits of organic matter;

19. Increasing ecosystems' ability to restore and maintain the natural balance.

The impact of the beaver on other animals

Beavers dig dens and canals, build dams and flood areas, and their activities initiate natural processes in wetlands. Collapsing dens form numerous loops and shallow areas that are overgrown by water and rush plants. The resulting meanders and shallow zones in coastal areas transform the original character and form of the shore line. The sites modified through beaver activities attract various animals. The aim of this study was to review publications that analyze the impact of beaver habitats on changes in the quality and quantity of local fauna.

Invertebrates

Ponds colonized by beavers offer a supportive environment even for the smallest aquatic organisms – the plankton. Plankton play an essential function in the food chain of every aquatic habitat. The ponds created by beavers significantly slow down the flow of water in rivers and increase water temperature. The above contributes to the development of plant and animal plankton. In a study of phytoplankton, zooplankton and zoobenthos communities colonizing watercourses in Leningrad and Novgorod oblasts, Pashchenko (2005) observed the highest number of aquatic species in the center of beaver ponds, and the abundance of plankton taxa decreased downstream of a dam. The positive impact and quantitative and qualitative characteristics of the influence of beaver activity on zooplankton in small river in Prioksko-Terrasnyi Nature Biosphere Reserve was presented by Dgebuadze et al. (2012).

Pliūraitė and Kesminas (2012) noted that the abundance of Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa in upstream forest sites in all streams was higher than in beaver ponds and downstream sites. Statistically significant differences were found in the absolute and relative abundance of EPT and Chironomidae between the analyzed stream sites. The absolute and relative abundance of pollution-sensitive taxa was significantly higher in forest sites than in beaver ponds or downstream sites in all examined streams. The absolute and relative abundance of Chironomidae was significantly higher in beaver ponds than in upstream forest sites and downstream sites. Plecoptera and Coleoptera were not determined in beaver ponds. The absolute abundance of Plecoptera was significantly higher in upstream forest sites than in downstream sites in all three streams. Gatherers were the predominant functional feeding group in terms of relative abundance in all examined habitats. The percentage of gatherers was higher in beaver ponds than in forest and downstream sites.

The accumulation of organic matter in beaver ponds and the resulting decrease in water flow rates create a supportive environment for many aquatic invertebrates, including mayflies (Ephemeroptera), caddisflies (Trichoptera) and true flies (Diptera). Those insects constitute a source of food for fish, amphibians, reptiles and birds (Bashinskiy 2009, Ciechanowski 2010). Slow water flow leads to changes in temperature, which contributes to the growth of invertebrates and changes in species composition as taxa characteristic of running waters are replaced with more abundant species that colonize stagnant water bodies (ponds). Total invertebrate biomass and density can be even five-fold higher in beaver ponds than in other parts of the watercourse where beaver activity is not observed.

Beaver dams create a highly supportive environment for larval development of many insect species. The upper part of the dam over which water flows is colonized by species characteristic of running waters (including members of the family Simulidae and order

Trichoptera). The base of the dam is often inhabited by larvae of insects that colonize bodies of standing water, including members of the family Culicidae and order Odonata (Brzuski and Kulczyka 1999).

Biotope changes induced by beavers can also benefit land-based invertebrates. Some insects, including *Drosophila virilis* fruit flies, lay eggs in rotting bark of selected tree species. Those reproductive requirements are readily met in sites situated in direct proximity of beaver habitats (Ciechanowski 2010). Beaver activities increase the availability of local microhabitats for rare insects that colonize and reproduce in dead wood and wood dust. Beavers utilize only a third of the cut trees and shrubs, and the remaining material is left to gradually decompose. Some trees dry up due to flooding, which makes beaver habitats additionally attractive for insects.

Beaver activities have been studied in an island on a lake in the northern Poland. The island abounds in aspen trees cut by beavers, and it is a habitat of the eyed squeaker (*Saperda perforate*), a beetle of the family Cerambycidae. Beaver habitats along a Bavarian stream also contributed to a significant increase in the abundance of the flat bark beetle (*Cucujus cinnaberinus*), a rare species listed in Annex II of the Habitats Directive (Zahner et al. 2006).

Bartel et al. (2010) studied the impacts of the North American beaver on the species diversity of plants colonizing coastal areas and the responses of *Neonympha mitchellii francisci* butterfly populations to beaver-induced changes in the environment. Beavers inhabited wetlands colonized by plant species not encountered in other coastal zones, and their habitats contributed to the diversity of plant species. The results of the cited study validated earlier theories concerning the effects of beaver activity on plant species diversity and demonstrated that beavers indirectly contribute to the survival of rare animal species by modifying the composition and increasing the diversity of plant communities in wetlands. The above authors demonstrated that the engineering activities of beavers can improve habitat availability, the composition of plant communities important for endangered insect species and preserve the diversity of plant species in a given habitat.

Beaver impoundments can potentially harm endangered freshwater pearl mussels. Beaver reintroduction schemes should account for conservation efforts addressing protected species, and critical river sections should be inaccessible to beavers to minimize their harmful impacts on rare and threatened lotic species (Gurnell et al. 2008).

Fish

Beavers considerably transform biological conditions in the colonized aquatic habitats. Beaver activities significantly influence the morphological structure of the river channel, sedimentation rates, organic matter storage, circulation of selected elements, water quality, nutrient transport and the quality of riparian habitats. Those transformations lead to changes in fish habitats, including the size and species composition of fish populations. In the same rivers and water bodies, beavers were found to exert both positive and negative impacts on fish communities (Parker and Rønning 2007).

After the introduction of the beavers, the state of the ichthyofauna in Negrylów Stream, which had suffered substantial degradation from forestry works, improved markedly. In comparison to analogous segments of other streams in the Bieszczady Mountains (SE Poland), fish density and biomass here were very high (Kukuła and Bylak 2010).

Lithuanian studies provided valuable inputs regarding the impact of beaver habitats on the species composition of fish populations. In Lithuanian trout streams, a total of 9 fish species were determined in sites not colonized by beavers. Streams intersected by beaver ponds were colonized by a higher number of 15 fish species. Stream sections not transformed by beavers were dominated by two species of trout, the stone loach and the gudgeon. Large chub and perch populations were additionally observed in beaver ponds. The above findings could suggest that beaver habitats contribute to the species diversity of ichthyofauna in the discussed region.

Variations were also noted in the average size of fish populations between the described types of stream. Higher fish biomass was reported in stream sections not colonized by beavers than in beaver ponds. The above studies also pointed to the negative impacts of beaver dams on streams inhabited by salmonids (Kesminas et al. 2013), including:

- inhibited migration and restricted fish habitats,
- reduced area of breeding grounds,
- damage to natural habitats in mountain springs.

Other researchers have confirmed that the size of fish populations and fish biomass are higher in areas flooded by beavers than in sections of the same rivers with a well-preserved riparian character (Dgebuadze et al. 2001). It should also be noted that beaver dams can disrupt fish migration routes and obstruct access to spawning grounds. The results of the cited studies demonstrate that researchers are divided over the influence of beaver habitats on the abundance and development of various fish species. Similar conclusions were formulated by Canadian researchers (Col-

len and Gibson 2001), who investigated the correlations between beaver and fish habitats and compared the environmental effects exerted by Eurasian and North American beavers.

Beavers exert direct and indirect effects on fish habitats that can have both positive and negative consequences, including:

a) positive effects:

• fostering a supportive environment for large fish;

• creating shielded and secluded areas where selected fish species can hide and forage for food;

• stabilizing and slowing down hydrological effects in beaver ponds, including erosion occurring at the bottom and on the sides of water channels and water bodies. Beaver impoundments regulate water flow and create favorable conditions for invertebrates and, consequently, fish;

• stabilizing water temperature. The gradual increase in the temperature of pond water can increase production in cold streams;

• in streams containing large amounts of mud and sediments, those fractions are captured and settled on the bottom,

• greater diversity and quantity of organic matter in water, which provides a source of food for invertebrates, fungi and microorganisms;

• intensified production of nutrients in beaver ponds increases productivity in ponds and downstream river sections;

• reduced acidity and neutralization of selected toxic compounds;

• creation of shelters.

b) negative effects:

• upstream migration may be obstructed by large dams or dams built in spillways;

• higher water temperature may be harmful for cold-water fish species that can survive within a narrow range of temperatures;

• silting up of fish spawning grounds;

• changes in the species composition of fish populations and the emergence of undesirable species;

• fostering a supportive environment for predators (predatory birds, mammals, fish) that pose a threat to desirable fish species in a given area.

Domagała et al. (2013) investigated the direct and indirect effects of beaver dams on the abundance of salmonids and the effectiveness of stocking the Sitna and the Pokrętna streams (NW Poland) with fish of the family Salmonidae. The above authors discovered that trout fry had been harvested along the analyzed stream sections before the construction of beaver dams. The examined watercourses were subsequently stocked with trout upstream of beaver dams, but fish harvesting levels remained low downstream of the dams. The results of the cited study indicate that beaver dams had contributed to the deterioration of biological and morphological parameters that condition the survival of salmonids, and they lowered the effectiveness of stocking measures. The drop in the abundance of salmonids can be attributed to the construction of beaver dams and the associated consequences, including changes in hydrological conditions, physical and chemical parameters, in particular higher water temperature, increased populations of fish characteristic of limnetic environments, including pike and perch, the emergence of predatory species that feed on fish fry and the accumulation of silt on the bottom of the streams.

Amphibians and reptiles

Beaver ponds serve as breeding grounds, foraging sites and shelters for amphibians and reptiles. Progressing environmental degradation around the globe dramatically reduces the abundance and geographic range of amphibians and reptiles. These negative changes are triggered by the disappearance of small water bodies, groundwater depletion, environmental pollution and other factors.

Beaver ponds play an important role in mitigating adverse environmental changes, in particular in areas that are less abundant in small or large bodies of standing water. The survival of amphibians is largely conditioned by the state of aquatic habitats. Many amphibian species burrow in mud in water bodies whose bottom does not freeze in winter. In spring, ponds and lakes offer breeding grounds for amphibians that lay eggs in warm and sun-exposed shallow areas shielded by plants and sunken tree branches. Amphibians hunt for invertebrates and their larva in ponds and their surroundings, and tadpoles forage on dead plants and animals in areas flooded by beavers. Beaver ponds overgrown by plants in the process of succession create a favorable environment for amphibians and reptiles.

The effect of Euroasian beaver activity on amphibian reproduction was studied in small river valleys in the Novgorod Oblast (Bashinskiy 2008). Amphibian reproduction rates were low in sites not colonized by beavers. In spring, beaver ponds warm up quickly, becoming attractive breeding grounds for amphibians. High reproduction rates and maximum abundance of tadpoles were observed in partially drained ponds, but high larval mortality rates were also often noted in those locations. Tadpole survival in flooded and empty ponds is determined by factors that are not associated with beaver activity, including geomorphology and climate.

Numerous observations (Andrzejewska-Wierzbicka and Bereszyński 2000, Derwich et al. 2007) have

revealed that beaver lodges provide shelter for grass snakes (*Natrix natrix*), and beaver dens are often colonized by various species of frogs, toads and crayfish. Beaver impoundments can thus contribute to the restoration of animal populations that are rare or locally extinct, in particular amphibians (Dalbeck et al. 2007).

Beaver ponds are also attractive habitats and breeding grounds for selected reptile species, including the grass snake (*Natrix natrix*) and the European pond turtle (*Emys orbicularis*). The growing abundance and expanding geographic range of beavers can stabilize reptile populations. The European pond turtle has a preference for small and shallow lowland bodies of stagnant water that are rapidly heated and overgrown with plants in the littoral zone. They include small lakes, oxbow lakes, swamps, peatlands, wet alder carr woodlands and permanent and seasonal marshes. Turtles also readily colonize silted, slow-flowing and meandering water courses such as streams, rivers, canals and wide drainage ditches (Devaux 2000, Wisler et al. 2008).

The results of the above studies indicate that the European pond turtle has a preference for habitats that are transformed by beavers. Direct correlations between turtle and beaver habitats have not been identified, but beavers definitely play or will play an important role in restoring the populations of the European pond turtle in Poland and other European countries.

A study of six beaver localities in the Bieszczady Mountains (SE Poland) revealed three reptile species (Derwich et al. 2007) as follows: slow worm (*Anguis fragilis*), grass snake (*Natrix natrix*) and common European adder (*Vipera berus*). Interestingly, the first two taxa colonized the analyzed sites only after they had been inhabited by beavers. The analyzed beaver ponds were inhabited by a total of five amphibian species: yellow-bellied toad (*Bombina variegata*), Alpine newt (*Triturus alpestris*), northern crested newt (*Triturus cristatus*), Carpathian newt (*Lissotriton montandoni*) and common frog (*Rana temporaria*). Some of the analyzed localities were also colonized by amphibians only after the establishment of beaver habitats.

Birds

The abundance of fish and invertebrates makes beaver habitats highly attractive for other animal species, including otters, minks, grey herons, black storks and other predatory mammals and birds. Lake islets, dead trees and natural structures create ample nesting grounds for many bird species. Wetlands and areas flooded by beavers are inhabited by various birds during breeding and migration seasons.

Beaver ponds significantly contribute to the abundance and diversity of bird species. Those effects are noted already in the first year after the construction of beaver dams, and they are stabilized in the successive three to four years. In areas colonized by beavers, the density of selected bird species can be even three-fold higher in comparison with surrounding territories that had not been transformed by beavers (Nummi and Pöysä 1997).

Beaver pond ecosystems create safe habitats for water and wetland birds during breeding, resting (molting) and migration seasons. Beaver ponds in woodlands act as breeding grounds for water birds due to an abundance of secluded areas, where birds can build their nests. Bird breeding success is considerably higher in beaver ponds than in surrounding areas. Beaver habitats are safe havens, where birds can breed in secluded nooks and visually isolated shelters. The environmental diversity of beaver ponds minimizes the threat of predatory attacks and increases the availability of food sources. Nutritionally rich beaver habitats encourage adult birds to incubate their eggs in those sites, and they also attract fast-growing juvenile birds (Brzuski and Kulczycka 1999). Beaver ponds thaw faster in spring, which speeds up bird nesting.

Beaver habitats are readily occupied by various duck species during the breeding season. The abundance and density of duck species have been found to be positively correlated with the surface area of the water table, the presence of shallow zones and the total length of the shore line overgrown with trees. The above requirements are met in most forest ponds colonized by beavers (Nummi 1989, Nummi and Pöysä 1997).

Studies investigating colonization patterns and the abundance of various duck species in beaver ponds revealed a significant increase in Eurasian teal (*Anas crecca*) populations in the first two years after the creation of beaver impoundments. No changes were reported in the abundance of mallard (*Anas platyrhynchos*) and Eurasian wigeon (*Anas penelope*) populations. A study of Swedish habitats demonstrated that beaver places were also readily inhabited by the common goldeneye (*Bucephala clangula*). Other researchers have confirmed the stabilizing effects of beaver impoundments on duck populations (Derwich et al. 2007, Nummi 1992, Rosell et al. 2005).

Dead trees in beaver ponds, wetlands and marshes are colonized by woodpeckers and other birds that nest in tree hollows. Trees offer shelter and breeding sites for birds, and they are also inhabited by insects that constitute a plentiful food source for birds.

Beaver activities transform plant communities that surround ponds. Beavers cut and chew on trees, which leads to the thinning of tree populations and intensive proliferation of shrubs. Those processes contribute to changes in the species composition of birds that

nest in those areas. Beaver habitats are generally accompanied by an increase in populations of singing birds characteristic of shrubby areas. The sedimentation of mineral and organic deposits decreases pond depth and leads to the formation of shallow zones that are readily used as foraging grounds by wading birds. Trumpeter swans (*Cygnus buccinator*) and Canada geese (*Branta canadensis*) often build nests on top of beaver lodges (Rosell et al. 2005). Predatory birds use dead trees in beaver ponds to keep vigil and hunt for prey.

Mammals

Beaver dams and lodges also deliver numerous benefits for mammals. Beaver activities can have varied impacts on mammalian habitats, and they enable mammals to:

- find shelter in beaver lodges and deserted dens,
- find shelter in areas transformed by beavers,
- forage for plants in beaver ponds and their immediate vicinity,
- prey on other animals in beaver habitats.

In the 1950s, the density of otter and American mink populations in the Białowieża Forest was positively correlated with the distribution of Eurasian beaver habitats (Żurowski and Kammer 1988, Sidorovich et al. 1996). Mink and otter habitats often overlap the territories colonized by beavers. Minks and otters prey on small mammals, fish, crayfish and amphibians in beaver ponds. Beaver lodges and dams provide shelters for otters. In winter, otters use ventilation holes that are created by beavers in ice covering ponds. A study investigating otter distribution patterns in the central Poland revealed a positive correlation between otter and beaver habitats. In the Region of Mazowsze, otter populations were twice higher in areas colonized by beavers than in territories, where no signs of beaver activity were detected. The above observations do not provide sufficient evidence to determine whether the noted correlation can be attributed to the environmental preferences of the analyzed species or the positive impact of beaver engineering activities. Some researchers had previously postulated the presence of a commensal relationship between the two species, whereby otters benefit from beavers' activity but do not affect beavers. Beavers are a keystone species that modifies the flow of matter in river ecosystems, influences primary and secondary production and contributes to habitat diversity by creating a supportive environment for invertebrates and fish. Otters inhabit beaver dens and lodges and hunt in the vicinity of beaver dams (Romanowski et al. 2010). North American river otters find shelter in beaver impoundments in winter. In Idaho, 38% of otter shelters were observed in dens dug by beavers. Researchers believe that the increase in Polish beaver populations has contributed to the restoration of otter communities. In Latvia, positive correlations between otter and beaver populations were observed by Ozolins and Rantins (1992).

Two interesting cases of coexistence of the Eurasian beaver and the European pine marten (*Martes martes*) were reported in Norway (Rosell and Hovde 1998). In the first case, two male martens and one female marten colonized a beaver lodge in winter. Beaver lodges are well insulated against cold, and the temperature inside a lodge is always higher than outdoor temperature. In the discussed case, pine martins inhabited a warm beaver lodge to conserve energy that would otherwise be used to maintain the required body temperature for survival.

In the second case, marten droppings were observed near a hole dug in snow covering a beaver lodge. The droppings contained fragments of beaver hair and claws. Based on the size of undigested remains, researchers concluded that the marten had killed and eaten a one-year-old beaver. The animal tracks discovered in snow also suggested that the beaver had not been attacked outside its lodge. The marten probably used the ventilation hole to enter the lodge and kill its inhabitant inside.

Beaver habitats also attract other predatory mammals that hunt for small animals, including raccoons (*Procyon lotor*), whose population is increasing steadily in Poland. Other predators find shelter in deserted lodges and dens that are located higher, among them the European badger (*Meles meles*), European pine marten (*Martes martes*) and red fox (*Vulpes vulpes*) (Rosell et al. 2005).

Beaver ponds are often surrounded by lush communities of herbaceous plants, shrubs and trees those provide ample sources of food for ungulates, such as roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and moose (*Alces alces*). Studies investigating correlations between beaver habitats and moose foraging habitats revealed that the two species compete for food. Beaver colonies relatively quickly damaged large aspens in the investigated site. The local tree stands were considerably thinned, which supported the growth of shrubs and root suckers those constitute highly attractive food for moose. Large moose communities that colonize a given habitat for long periods of time can rapidly deplete young trees and root suckers before they can develop into trees, thus depriving beavers of a primary food source. For this reason, the coexistence of beavers and moose is possible only when their populations are relatively low in shared and neighboring habitats (Brzuski and Kulczycka 1999).

Balčiauskas and Ulevičius (1995) showed that making burrows, houses and ponds, beaver improve environmental conditions for other semi-aquatic mammals. A lot of beaver burrows in sandy shores give refuges for otters and minks. Partly due to the beaver activity, the density of these species was high (3.6 and 10.95 respectively per 10 km of shoreline).

Sidorov et al. (2011) have argued that beavers face competition from species those forage on stalks and shoots of aquatic plants and chew on herbaceous plants, shrubs and trees growing on land at the distance of 100-150 m from the shore. In winter, significant competition may be observed in areas characterized by low food supply and high density of other semiaquatic species, including muskrats (*Ondatra zibethicus*) and water voles (*Arvicola amphibius*). Competition from muskrats is most intense in fall and spring, when the species forages on stalks and shoots of aquatic plants those constitute a source of food for beavers. In fall, winter and early spring, European hares (*Lepus europaeus*) and mountain hares (*Lepus timidus*) feed on the branches of trees cut by beavers. Hares chew on tree boughs and branches protruding above snow cover, whereas murids feed on material buried under the snow. Those species compete for food only in years, when their populations are particularly high. Significant competition is posed by moose and red deer, especially in conservation areas. Moose forage on willows in the riparian zone of ponds and lakes, and they can cause extensive damage to those trees. Their competitive influence is most strongly felt by beavers in late fall and winter. Moose select the bark and shoots of woody plants, and in winter, they b continue debarking of trees cut by beavers. Beavers also compete for food with farm animals, including goats, cows and horses. Farm animals can contribute to the collapse of beaver dens.

Beaver impoundments attract other small semiaquatic animals, including muskrats and water voles. In some cases, muskrats co-inhabit beaver lodges and partake of food stored by beavers. The relationship between beavers and muskrats is an example of commensalism (where one species benefits from the other without affecting the latter) that exists in sites transformed by beavers.

In Germany, 14 out of 20 investigated beaver habitats were visited by wild boars those scavenged for water lily and reed stems in dry parts of beaver ponds. Wild boars also took mud baths in shallow pond zones to cool down and get rid of external parasites. Dead and dying trees in beaver ponds or in their vicinity are also colonized by bats those find shelters under patches of dry bark protruding from trunks.

Ponds and woodland corridors cleared by beavers create feeding sites for bats due to an absence of obstacles those inhibit flight and echolocation. Those sites attract insects that breed in water, swarm over its surface and provide an ample source of food for bats. A study of Eurasian beaver habitats in small streams intersecting forests in northern Poland revealed a significantly higher number of bat passes (*Pipistrellus nathusii*, *P. pipistrellus*, *P. pygmaeus*, *Nyctalus noctula* and total passes for all bat species) in stream sections modified by beavers (flooded and subjected to intensive tree cutting) than in unmodified sections. The activity of *Myotis* species was significantly lower along the transect containing the largest beaver ponds, possibly due to the presence of duckweed blankets (Lemnaceae) those produce clutter echoes and reduce prey detection by echolocation (Ciechanowski et al. 2011).

The previously cited study of six beaver localities in the Western Bieszczady Mountains also revealed the presence of numerous mammal species in the vicinity of beaver habitats (Derwich et al. 2007). Some of them appeared the analyzed area only after it had been inhabited by beavers, including following: *Pitymus subterraneus*, *Plecotus aurilius*, *Arvicola terrestris*, *Pipistrellus pipistrellus*, *Mustela nivalis*, *Myotis myotis*, *Clethrinomys glareolus*, *Ondatra zibethicus*, *Sorex alpinus*, *Neomys anomalus*, *Neomys fodiens*, *Capreolus capreolus*, *Sicista betulina*, *Lutra lutra*, *Crocidura leucodon* and *Crocidura stuaveolens.*

The above study demonstrates that beaver impoundments significantly contribute to the abundance and diversity of mammal species. Each of those animals, beginning from small pigmy shrews to large species, such as roe deer, were able to benefit from beaver activities to suit their own survival needs.

Beavers as prey

Beavers establish symbiotic and commensal relationships with other mammals, but they can also be pursued by large predators. In Latvia, beavers accounted for 6.4% of the biomass in the diet of wolves, and they were the third most common species of prey pursued by wolves. Beavers fell prey mostly to wolves younger than one year as well as adult predators. Wolves aged 1-2 years were less interested in the analyzed rodents. Male wolves were significantly more likely to prey on beavers than females. Mertc (1953) and Rjabov (1993) argued that the loss of beaver populations resulting from wolf predation can be as high as 14%. In Baltic countries, beavers are also exposed to predation pressure from other large predators and humans (hunting).

Wolves are generally the only predators that directly attack beavers. A successful fox attack on a two-month-

old beaver female was reported in the southern Norway (Kile et al. 1996). During the incident, one of the adult individuals made attempts to ward off the enemy by slapping its tail on the water. The share of young beavers in the diet of foxes was investigated in Belarus. During a field study, the remains of young beavers were found directly at the site of a predatory attack in eight cases, and near exits from fox dens in 30 cases. Two thirds of such cases were noted in July, and one third – in August (Sidorovic and Sidorovic 2011).

In Russia, the main predators those pose a threat to beaver populations are wolves (58%), stray dogs (27%) and lynxes (15%) (Glushkov et al. 2001). Other animals that prey on beavers include bears, otters and foxes, and young beavers - from large pikes (*Esox lucius*) and taimen (*Hugo taimen*, Salmonidae)

According to Sidorov et al. (2011), the primary predators of beavers in the Omsk Oblast are wolves, wolverines, lynx, bears and stray dogs. Otters were not found to directly attack beavers. In the late 1940s, beavers accounted for 5.3% of wolf diets in summer and 15.3% in winter the Voronezh Biosphere Reserve. In the Arkhangelsk Oblast, young beavers face danger from foxes, raccoon dogs, minks and martens. In the Khoper Nature Reserve, two lethal attacks on one-year-old beavers were perpetrated by foxes. Feral dogs hunt down beavers directly in their shelters. The remains of beavers with estimated body weight 2-2.5 kg were reported in eagle-owl pellets in the Arkhangelsk Oblast and the Voronezh reserve.

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ЕВРОАЗИЙСКИЙ БОБР (*CASTOR FIBER*) КАК КЛЮЧЕВОЙ ВИД – ЛИТЕРАТУРНОЕ ОБОЗРЕНИЕ

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Резюме

Евразийского бобра *Castor fiber* можно считать ключевым видом, т.е. таким, влияние которого на структуру и функционирование экосистем является непропорционально большим по отношению к его численности или биомассе. Разнообразие ролей, которые бобр играет в экосистемах, часто становилось предметом научных исследований. Целью нашей работы было обобщить литературные данные, касающиеся взаимосвязи между существованием бобров и изменениями качественных и количественных показателей местной фауны.

Ключевые слова: Евразийский бобр *Castor fiber*, влияние, биоразнообразие