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**IMPACT OF THE KEYSTONE SPECIES,
THE EURASIAN BEAVER (*CASTOR
FIBER*), ON HABITAT STRUCTURE
AND ITS SIGNIFICANCE TO
MAMMALS**

Doctoral dissertation

Biomedical Sciences, Ecology and Environmental Science (03 B)

Vilnius, 2016

The dissertation was prepared in 2011-2015 in Vilnius University.

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INTRODUCTION

The Eurasian beaver (*Castor fiber*) is one of the two beaver species belonging to genus *Castor* (Лавров, 1981). Both the Eurasian and North American beavers (*Castor canadensis*) are the largest rodents in the Palearctic. In the early 20th century, beavers were almost extinct throughout their range. By the 1900s population of the Eurasian beaver decreased from 100 million to 1000 individuals, while in North America from 60 million to several thousands of individuals. The main cause was the hunting for fur, for glands and because of human-beaver conflicts in agriculture and forestry (Novak, 1991). However, after the successful conservation efforts that started in 1920's in North America and in Europe, nowadays beavers have restored their previous range only partially (Halley, Rosell, 2003).

The history of Eurasian beaver is well documented in Lithuania. According to Prūsaitė (1988), beaver was extinct in Lithuania in the beginning of 20th century. No permanent residents were found and only the migrants from the upper basin of Nemunas were observed. The reintroduction program of the beaver started in 1947 by the initiative of T. Ivanauskas. First beavers were released in Žuvintas. After the 1947, a few more attempts were made in different regions of Lithuania. Since the 1970s, beaver is found in most Lithuanian rivers (Prūsaitė, 1988). According to Ulevičius (2008), there could be about 80-100 thousand of beavers in Lithuania.

Beavers play important role in ecosystems and is considered a keystone species (Davic, 2003). Due their ability to modify the landscape, beavers are considered to be ecosystems engineers (Jones *et al.*, 1994; Gurney, Lawton, 1996; Müller-Schwarze, Sun, 2003). According to Johnston and Naiman (1990a), beavers can change up to 4% of the landscape over a decade. Beavers convert the dry land to wet meadows, ponds and various types of marshes. In this way, the heterogeneity of the landscape and carrying capacity is highly increased

(Remillard *et al.*, 1987; Johnston, Naiman, 1990b; 1992). Due to changed environmental conditions, the community structure of plants and animals do experience significant changes in the areas associated with beaver sites. Due to selective grazing and changes in moisture regime, the abundance of some plant species may greatly decrease (Nolet *et al.*, 1994). Sometimes it leads to extinction of these species on local scale (Johnston, Naiman, 1990b). According to Rosell *et al.* (2005), browsing by beaver considerably changes the species composition of the plant community towards domination of the non-preferred species. Although the decrease of plant species richness may be significant in some places on the local scale, on the landscape scale the species richness increase can occur (Wright, Jones, 2002).

The changes in the composition and structure of plant communities could have an impact on ungulates, especially in winter (Safonov, Saveljev, 1992; Danilov, 1995). Due to decreased competition, increased moisture and sunlight, the communities of willow species (*Salix* spp.) develop in ecotones of beaver wetlands (Hodkinson, 1975). Also, browsing by beaver may accelerate the regrowth of aspens (*Populus* spp.). By cutting aspens, beaver creates unshaded patches in the forest and stimulates the regrowth of adventitious buds by the roots, which sprout around the base of the cut plants (McGintley, Witham, 1985). Both, willow and aspen species are very important in the winter diet of roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and elk (*Alces alces*) (Safonov, Saveljev, 1992; Danilov, 1992, 1995).

Habitats created by beavers may play important role for semi-aquatic mammals. Muskrats (*Ondatra zibethicus*), water voles (*Arvicola terrestris*), American minks (*Neovison vison*) and otters (*Lutra lutra*) visit or even live in beaver ponds (Knudsen, 1962; Sidorovich *et al.*, 1996). Beaver habitats provides food, stable water level and shelter for these species. American mink (*Neovison vison*) and otter (*Lutra lutra*) hunt for prey – fishes, amphibians, small mammals and even beaver cubs – in beaver ponds (Bailey, Stephens, 1951). Muskrats and

water voles may feed on remains left by beaver (Grasse, 1951). All these semi-aquatic species use beaver lodges as shelters (Leighton, 1933; Grasse, 1951; Tyurnin, 1984; Müller-Schwarze, 1992).

Though the impact of beaver to habitats, landscape and plant / animal communities is well studied in North America, only some studies were done in Europe. There is lack of data on the impact of Eurasian beaver on landscapes (Törnblom *et al.*, 2011), as well as the significance of the beaver-modified habitats to mammals and significance of beaver-made structures, especially beaver burrows and beaver lodges.

The population of the Eurasian beaver is very dense in Lithuania (Ulevičius, 2008) and could be considered as one of the densest in Europe (Halley, Rosell, 2003). High density of beavers suggests intensive impacts on landscape, as well as impacts on mammal communities. Here, in this study, special attention was paid to the less studied aspect of beaver impact on mammals – building and burrowing activity of this keystone species. Beaver lodges and beaver burrows are quite numerous and fairly permanent elements of habitat infrastructure in the beaver-modified areas (Ulevičius *et al.*, 2009; Lamsodis, Ulevičius, 2012), and scarce earlier studies have demonstrated their significance to small mammals (Барабаш-Никифоров, 1950; Ulevičius, Janulaitis, 2007).

Besides building activity of beavers, we also have evaluated the use of beaver wetlands by mammals of different ecological groups. Beaver wetlands are specific and fairly natural habitats that have appeared in the Lithuanian landscape, which was highly transformed by draining activities and relatively intensive agriculture.

Finally, we evaluated the fitness of mammals that most intensively inhabited the environments transformed by beavers. For this task, we used the helminthological status of two small mammal species typical for the forest, but at the same time intensively occupied beaver wetlands.

The aim and objectives of the study

The aim of the study was to evaluate the scale of the effect of the Eurasian beaver to habitat structure, the significance of beaver-modified habitats and beaver-made infrastructure elements (beaver lodges and beaver burrows) to species diversity, abundance and distribution of mammals and to evaluate the population and helminthological status parameters of resident mammals in beaver-modified habitats.

The objectives of the study:

1. to quantify the impact of the beaver to habitat structure in an ecosystem by using remote and *in situ* mapping methods;
2. to evaluate the significance of beaver-modified habitats to diversity, abundance, distribution and community structure of mammals of different ecological groups;
3. to evaluate the significance of beaver-made structures (beaver lodges and beaver burrows) to carnivores, semi-aquatic and small mammals, while controlling for influencing factors (habitat, season, time of day);
4. to evaluate the demographic and helminthological status parameters of small mammals in beaver-modified habitats.

The novelty of the research

The scale of impact of Eurasian beaver (*Castor fiber*) on habitats and their structure was evaluated for the first time in an anthropogenized hilly morainic landscape where the density of beaver sites is extremely high and abundance is near carrying capacity. I developed a new method of geographic information system (GIS) based remote estimation of beaver impact to habitats, which was supported with *in situ* measurements.

Significance of beaver-modified habitats to mammals of different ecological groups was evaluated to distinguish species or groups of species of

mammals that benefit from habitat structure modifications by beavers in a hilly morainic landscape of eastern Lithuania.

Significance of the beaver-made structures (beaver lodges and beaver burrows) for mammals was evaluated using snow tracking, snap traps and infrared (IR) camera traps. The last method was used for the first time in researching mammal use of beaver burrows.

Demographic and helminthological status of the bank vole (*Clethrionomys glareolus*) and the yellow-necked mouse (*Apodemus flavicollis*), the species most associated with the beaver-made structures, were studied to evaluate changes in population and helminthological parameters that were possibly induced by beaver modifications of environment.

Defended statements

1. The Eurasian beaver, in conditions of abundant population, significantly affects the habitat structure of the hilly morainic landscape by creating and maintaining specific habitats and elements of habitat infrastructure. Contribution of the beaver-transformed wetlands to the overall habitat structure by area and share of ecotones is nearly comparable to that of the forest and open habitats.

2. Abundance of large and mid-sized mammals in beaver-affected habitats is similar in comparison to the forest habitat, but higher than in the open and mosaic habitats. Beaver-transformed wetlands are more attractive habitats for the species that are typical to fragmented landscape. Diversity of large and mid-size mammals in beaver sites is similar to that in the other habitats.

3. Beaver burrows are important habitat infrastructure elements for a number of mid-sized and small mammals. Significance of beaver burrows for these mammals differs depending on season. Beaver lodges attract small mammal species that are the typical of forest habitats.

4. Beaver alterations of habitat infrastructure weakly influence demographic parameters of dominant *Clethrionomys glareolus*. Use of the beaver-

transformed environments by *Clethrionomys glareolus* and the *Apodemus flavicollis* (two small mammal species typically inhabiting forest habitats) does not lead to significant changes of their helminthological status.

Approvals of the thesis

The results of the dissertation are published in four peer reviewed journals, two are listed in the Thompsons Reuters Web of Knowledge (ISI). The results were presented at eight international conferences:

1. two presentations in 5th International Beaver Symposium, Dubingiai, Lithuania 2009;
2. 8th Baltic Theriological Conference, Palanga, Lithuania, 2011;
3. two presentations in 6th International Beaver Symposium, Ivanic-Grad, Croatia, 2012,
4. 2nd International Symposium of Hunting, Novi Sad, Serbia, 2013;
5. 9th Baltic Theriological Conference, Daugavpils, Latvia, 2014;
6. 6th International Symposium: Dynamics of game animals populations in Northern Europe, Kirkkojahti, Republic of Karelia, Russia, 2014;
7. Methoden der Wildtierforschung (Methods of Wildlife Research), Bad Blankenburg/Thüringen, Germany, 2015.
8. 7th International Beaver Symposium, Voronezh, Russia, 2015.

1. REVIEW OF LITERATURE

1.1. The beaver (*Castor* sp.)

Only two species of beavers, the Eurasian beaver (*Castor fiber*) and the North American beaver (*Castor canadensis*), belong to genus *Castor*. The genus of true beavers originated in Eurasia and the ancestors of *Castor canadensis* migrated to North America in Pliocene epoch (Lavrov, 1983).

Both species are similar morphologically and behaviorally (Novak, 1987). The North American beaver is so similar to the Eurasian beaver that they were originally considered conspecific (Hill, 1982). The same ecological conditions are required for both species to inhabit an area: similar size of the water body, water level, river flow rate, plant species for diet and etc. However, due to differences in karyotypes, successful interbreeding between both species is impossible (Lavrov, Orlov, 1973).

The main differences between both species occur in building activity. According to Danilov and Kan'shiev (1982), the building activities of the North American beaver are more frequent than Eurasian. In northwestern part of Russia, the share of settlements of the North American beaver with dams and lodges was greater than the settlements of the Eurasian beaver (Danilov, 1995; Данилов и др., 2007). Although comparative studies have found the Eurasian beaver to be a poorer builder than the North American beaver, the effects of their dams on the environment will not be much different (Nolet, 1996).

According to Macdonald et al. (1995), the studies of North American beaver can provide important clues about the potential effects of Eurasian beaver. This is important because nearly all the information on the beaver's impact on the environment originates from studies of the North American beaver (Macdonald et al., 1995; Nolet, 1996). Where the Eurasian beaver construct dams and fell trees, they likely have similar effects to the landscape like the North American beaver (Macdonald et al., 1995).

1.2. The Eurasian beaver (*Castor fiber*)

1.2.1. Distribution of the Eurasian beaver

The Eurasian beaver is not equally distributed throughout the range of the species (Fig. 1). The continuous distribution is in the range from northern Poland through the Baltic countries to central Siberia. Large disjunct populations are registered in Norway and Sweden. Many small populations are scattered in western part of Europe (Halley, Rossel, 2003; Halley *et al.*, 2012).

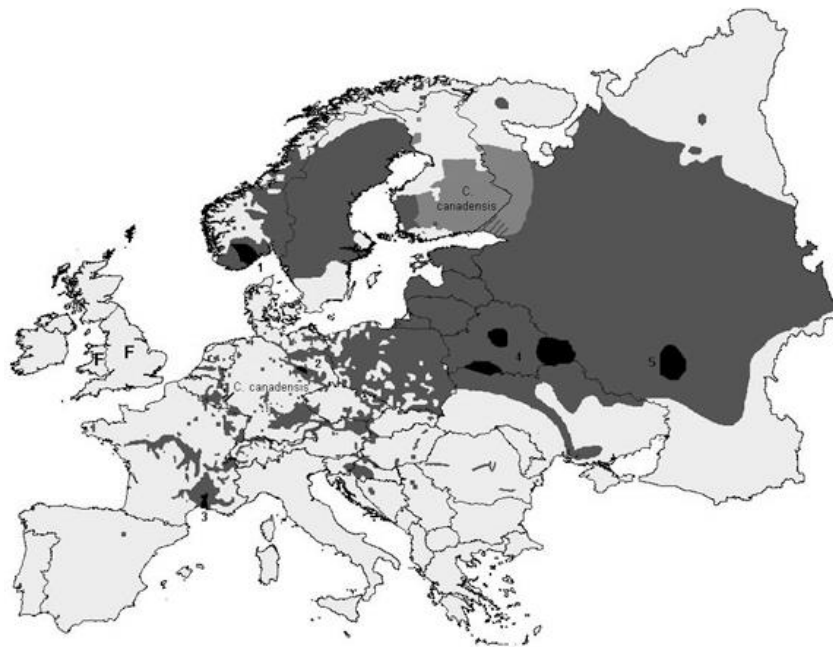


Figure 1. Distribution range of Eurasian beaver (*Castor fiber*) and North American beaver (*Castor canadensis*) in Europe. Traditional subspecies designations: 1 – *Castor fiber fiber*, 2 – *Castor fiber albicus*, 3 – *Castor fiber galliae*, 4 – *Castor fiber belarusicus*, 5 – *Castor fiber osteuropeus*. Dark grey shadings represents the present range of *Castor fiber* (locations of relict populations are marked in black); light grey shading represents the range of *Castor canadensis* (from Halley *et al.*, 2012).

As mentioned before, the Eurasian beaver was extinct in Lithuania in the beginning of 20th century. Almost 70 years have passed after the successful reintroduction of the Eurasian beaver in Lithuania. Continuous growth of the population size was documented from the beginning of the reintroduction (Fig. 2). There is a discussion of possible size of the beaver population in Lithuania (Ulevičius, 2010). According to the official census, the size of the beaver population could be in range from 50 to 60 thousands of individuals. According to the estimation of experts, it could reach more than 100 thousands of beavers (Ulevičius, 2010).

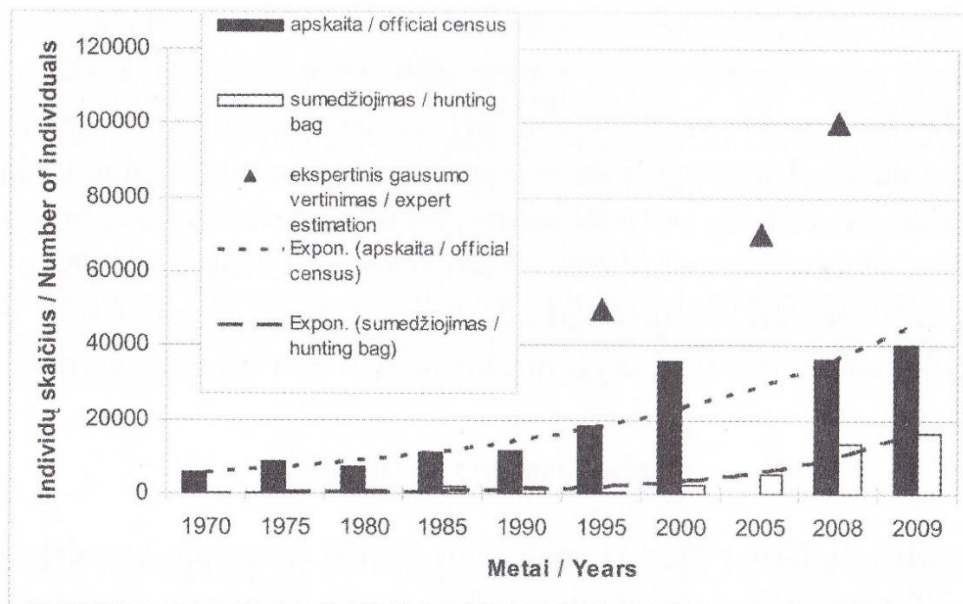


Figure 2. Beaver population dynamic in Lithuania in 1970-2009 (after the expansion) by the official census, hunting bag data and the data of expert estimation in 1996, 2004, 2008 (Ulevičius, 2010).

Eurasian beaver is widely distributed throughout all territory of Lithuania (Fig. 3) (Balčiauskas *et al.*, 1999; Ulevičius, 2008). It can be found in all rivers of Lithuania. However, abundance of beavers is different in various parts of Lithuania, and it depends on the landscape (Bluzma, 2003; Ulevičius, 2008). The

more dense population of beaver is found in north-western and eastern parts of Lithuania, in Plungė, Telšiai, Kelmė, Trakai, Rokiškis and Molėtai districts, where hilly morainic landscape is common (Ulevičius, 1999). The estimated density of beavers can be up to 20 beaver sites per 1000 ha in those regions (Bluzma, 2003, Ulevičius 2008). In central and southern parts of the country, where plains are more common element of the landscape, the density of the beaver sites is significantly lower: 1 beaver site per 1000 ha. The average density of beaver sites in Lithuania was 4.12 beaver sites per 1000 ha and 0.8 beaver dam per 1 kilometer of the stream and drainage ditches (Ulevičius, 2008).

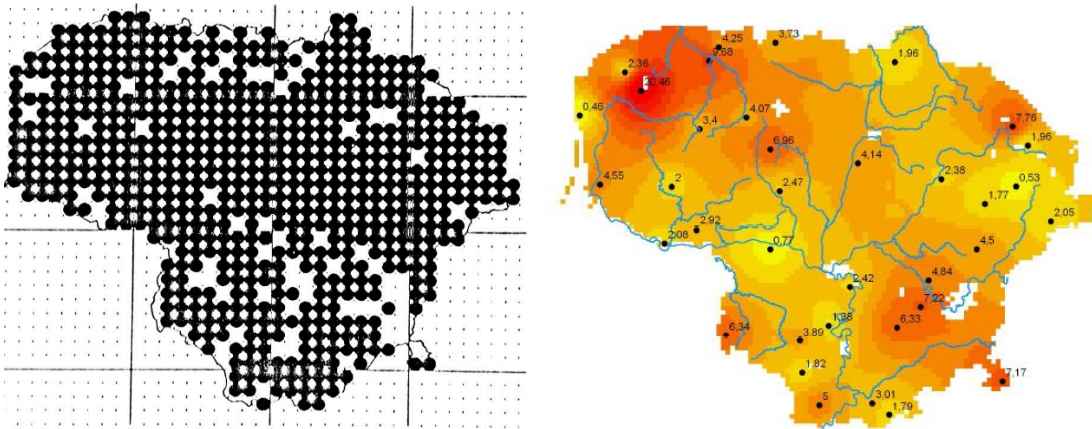


Figure 3. Distribution (left; Balčiausias *et al.*, 1999) and population densities (beaver sites per 1000 ha) (right; Ulevičius, 2008)) of the Eurasian beaver in Lithuania.

The distribution of Eurasian beaver among the habitats depends on the landscape structure and hydrographic network, which determines the quality of habitat (Collen, Gibson, 2001). The Eurasian beaver inhabits various types of water bodies, but prefers deep rivers and streams with slow flow and steep shores. The preference increases with increasing density of deciduous vegetation. In Lithuania, in 1980s, the majority of the beavers were inhabiting rivers. According to Prūsaitė (1988), two-thirds of the beaver's population inhabited natural rivers

and the remaining part – in the lakes, wetlands and drainage ditches. According to studies carried out in Lithuania, the greatest proportion of beaver population is settled in drainage ditches (36% of total beaver sites in Lithuania) in 2008. The estimated proportion of beaver sites in natural waters is 30%, in lakes is 16.5%, in various wetlands is 14.5% and in other habitats is 3% (Ulevičius, 2008). In hilly morainic landscape in eastern part of Lithuania, majority of beavers inhabit depressions between the hills (personal observation). This distribution could be determined by the insufficiency of natural rivers (rivers comprise 18% of hydrographic network in the region) and drainage ditches (due to unfavorable landscape for farming).

1.2.2. Ecology of the Eurasian beaver

Family and territory size. Beavers are monogamous animals (Müller-Schwarze, Sun, 2003). Beavers may live in families from 3 to 9 individuals or in pairs or singly (Дьяков, 1975). Sometimes up to 13 individuals are recorded in one beaver family. Commonly, families consist of one adult male and one adult female, two two-years and two one-year kits. In early spring, two-year old beavers leave the home after the newborns are born (Prūsaitė, 1988). According to Rosell and Parker (1996), the number of beavers in one beaver site is estimated to be an average of 3.8 individuals.

Beavers occupy various types of habitats – natural rivers, drainage ditches, lakes, wetlands and anthropogenic ponds (Prūsaitė, 1988; Collen, Gibson, 2001; Ulevičius, 2010). In linear habitats, like rivers and ditches, the home range of the beaver family is 0.5 to 12.8 kilometers of the shore and depends on both the landscape and density of the beavers (Macdonald *et al.*, 1995). According to Ulevičius (2010), the home range varies from 500 to 600 m to 1 km of the shore in territories with high beaver densities, while in less dense areas – up to 5 km. Meanwhile Herr and Rosell (2004) reported a home range of up to 4000 meters of

shore of one beaver family in Norway. In non-linear habitats like lakes and wetlands, an average home range had a radius of 0.8 km around the lodge (Aleksiuk, 1968).

Diet and feeding behavior. Beaver diet depends on both season and plant composition of the beaver's habitats (Jenkins, 1979; Müller-Schwarze, Sun, 2003). The bark of trees and shrubs becomes the dominant dietary components of the beavers during the cold season, when the green vegetation is absent (Jenkins, 1979; Haarberg, Rosell, 2006). In summer, the share of herbaceous and aquatic plants increases (Müller-Schwarze, Sun, 2003). The variety of plant species, on which the Eurasian beaver feeds is great, and the major share of beaver diet consists of 6 to 10 tree species. In all regions, the priority is given to willow (*Salix* spp.), poplar (*Populus* spp.), hazel (*Corylus* spp.), oaks (*Quercus* spp.), mountain ash (*Sorbus* spp.), maples (*Acer* spp.) and grey alder (*Alnus incana*) (Hall, 1960; Curry-Lindahl, 1967; Jenkins, 1979; Johnston, Naiman, 1990b; Nolet et al., 1994; Donkor, Fryxell, 1999; Haarberg, Rosell, 2006).

Both beaver species, Eurasian and North American, are central-place forager herbivores (Jenkins, 1979; 1980). As a central-place herbivore, beaver moves out from the water to select and cut the tree and transports it back to water. Transported plants may be eaten immediately or stored e.g. for winter (Jenkins, 1980; McGinley, Whitham, 1985; Basey *et al.*, 1988). The selectivity, both on size of the tree and on species, as the foraging distance from the shore increases. The diameter of cut trees decreases the farther it is from the shore. The same situation is with preferable plant species. Beaver spends more time on shore or goes farther for more favourable species (Jenkins, 1980; Donkor, Fryxell, 1999; Haarberg, Rosell, 2006).

1.2.3. Beaver built structures

All beaver built structures are grouped in two categories: 1) living structures (such as beaver burrows, lodges, semi-lodges) and 2) other building

activities (such as dams, canals, tunnels, tranches, and food caches) (ДЪЯКОВ, 1975).

Beaver dams. Beaver builds dams to increase the water level of the surrounding area. The increased water level deepens the water body, which is important for making food caches for winter, and covers the entrances to beaver burrows and lodges.

Dams (Fig. 4) are built in flowing water systems (small rivers, drainage ditches). The first dam is built immediately after the beaver moves in. The dam is not always fully established immediately following occupation of the water body; however, it is regularly reinforced the autumn of that year (ДЪЯКОВ, 1975). The repairing of the dam can be carried out in any time of the year, even in winter when the temperature of the air drops below -20°C (ПАРОВЩИКОВ, 1960; ДЪЯКОВ, 1975). Dam building/repairing is stimulated by the sound of flowing water when the dam is breached or destroyed (Wilsson, 1971).



Figure 4. Beaver dam (photo by A. Samas).

Beaver dams are built from various sizes of tree trunks, mud and small stones (Дьяков, 1975; Woo, Waddington, 1990). According to Дьяков (1975), tree trunks in diameter up to 20 to 25 cm are used for dam building. The size (length and height) of the beaver dam depends on the relief the river is flowing through and from the width of the river (Gurnell, 1998). In most cases, the dams of the Eurasian beaver do not exceed 30 meters in length, 0.8 to 1.3 meters in height, 2 to 2.5 meters in width at the base and 0.6 meters width and the top (Дьяков, 1975).

The number of beaver dams per one beaver site may vary from 1 to 10 dams (Ulevičius *et al.*, 2009). The number of dams depends on the slope of a stream, density of the beavers and human disturbance (Дьяков, 1975; Naiman *et al.*, 1986; Gurnell, 1998).

The food cache. The food cache (Fig. 5) or a storage is a pile of tree branches in the deepest part of the beaver pond. Often it is stacked near the beaver lodge or main beaver burrow with the nest chamber. The lower part of the cache comprises almost 2/3 of its volume and consists of shortest branches and twigs (up to 1.5 m). Meanwhile the upper layer is built from the longest branches (Dzieciolowski, Misiukiewicz, 2002). The size of the food cache depends on the size of the beaver family (Osmundson, Buskirk, 1993).

The species composition of stored plants depends on the surrounding vegetation (Busher, 1996; Dzieciolowski, Misiukiewicz, 2002). Busher (1991) found a positive association between the availability of species and its share in the food cache. Willows (*Salix* spp.), birches (*Betula* spp.) and hazel (*Corylus avellana*) comprise the greatest share of the plant species stored in the cache. Sometimes, species, that are non-preferred by beaver, like pine (*Pinus sylvestris*) and black alder (*Alnus glutinosa*), may be stored to stabilize the cache (Busher, 1996).



Figure 5. Winter food cache of Eurasian beaver (photo by A. Samas).

Beaver burrows. Beaver burrows are the main shelters of beavers (Дьяков, 1975; Erome, 1984). Two types of beaver burrows are distinguished: permanent (beaver burrows with nesting chamber) and temporal (used for feeding and hiding) (Дьяков, 1975; Gurnell, 1998). The entrance to the burrow is 0.75 to 1.5 meters under the water surface (Prūsaitė, 1988). The mean height of the burrow is 40 cm and mean width is 50 cm. The length of the burrow may vary from few to 20 meters (Ulevičius *et al.*, 2009) or even 100 to 200 meters (Дьяков, 1975). Temporal beaver burrows are shorter in length (1 to 3 m) while permanent are longer (Дьяков, 1975). The nesting chamber, situated at the end of the burrow, is a specific element of the permanent beaver burrow. The nesting chamber is typically 0.3 to 0.7 m above the upper edge of the burrow entrance, not deeper than 30 to 60 cm from the surface, about 1 m in width, and 0.4 to 0.5 m in height and lined with wood chips (Дьяков, 1975; Prūsaitė, 1988; Gurnel, 1998).

Beaver burrows have four main configurations: simple, branchy, U-shaped and combined (Fig. 6) (Ulevičius *et al.*, 2009). Simple and branchy shape burrows

are common to relatively young beaver sites or to beaver sites with solid ground shores, while U-shaped and combined burrows are typical to old beaver sites in drainage ditches of the peat bog. Therefore, the complexity of the burrow's system increases with the age of the beaver site.

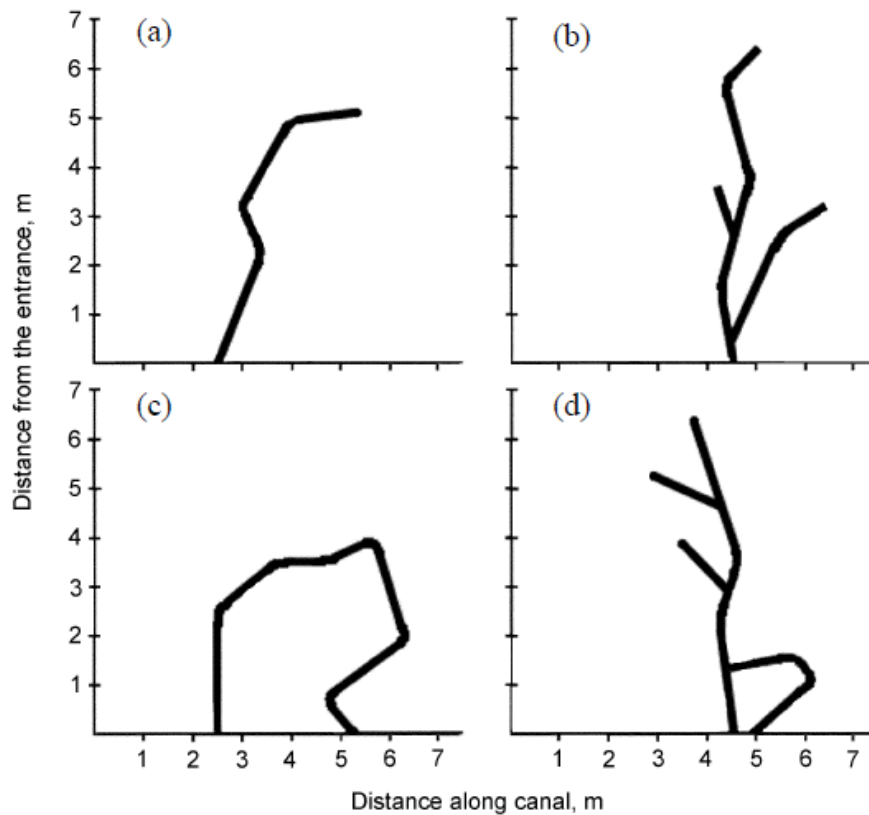


Figure 6. Four main types of beaver burrow configuration in canals of land reclamation: (a) - simple, (b) - branchy, (c) - U-shaped, (d) – combined (Ulevičius *et al.*, 2009).

The majority of beaver sites have beaver burrows or the signs of burrowing activities (collapsed beaver burrows). The density of beaver burrows depends on the slope of the shore and the type of the soil (Erome, 1984; Gurnel, 1998). Most frequently, burrows are found in rivers and drainage ditches and less often in self-contained beaver wetlands. The abundance of beaver burrows may vary at

different beaver sites. In drainage ditches of middle Lithuania, density of beaver burrows may reach up to 50 burrows per 1 km of ditch bed (Ulevičius et al., 2009).

Beaver lodges. Two types of beaver lodges are common: true lodges (Fig. 7) and semi lodges. True lodges are built in the areas flooded with water while semi-lodges – on the shore on the collapsed beaver burrow with the nesting chamber (Дьяков, 1975).

According to Федюшин (1935) and Wilsson (1971), beaver lodges may be built under two circumstances: 1) there are no suitable places to burrows and 2) when the water level rises in the burrows and submerges the nest.



Figure 7. Beaver lodge (photo by A. Samas)

True lodges are structures built farther from the shore that the base of the lodge is immersed. They are built from the same materials as the beaver dam (except the stones) and have shape of the cone (Дьяков, 1975). According to the author, the size of the lodges may varie in great range, but commonly beavers build lodges up to 1.8 meters in hight and up to 4 meters in diameter. After the lodge is built, beaver makes chambers in side of it. Up to 6 chambers could be made in one lodge (Fig. 8) (Ulevičius, Juškaitis, 2005). The nesting chamber is in the upper part of the lodge. It has ventilation through loosely arranged branches. In addition, holes and cavities of various sizes appear in the walls as a consequence of building the lodge. The thickness of the lodge walls are about 40 to 50 cm (Buech *et al.*, 1988).

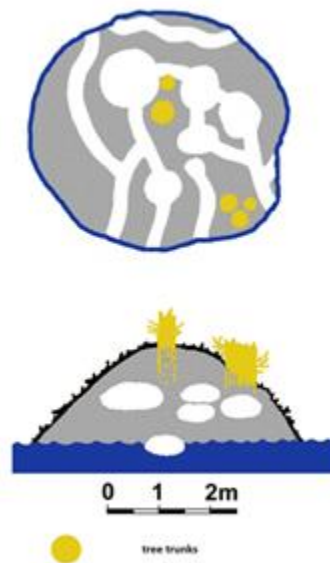


Figure 8. Structure of a beaver lodge (from Ulevičius, Juškaitis, 2005).

Around the lodge, beaver digs a ditch of 1.5 meters in depth. The entrance to the lodge is always under water. The average diameter of the base is 5 m, the height – up to 2 m (Prūsaitė, 1988). Sometimes one beaver lodge could be built from two or three lodges by joining them together. In such case, the diameter of

the lodge increases significantly, up to 10 meters. Two or three tops could be visible (Fig. 9) (Zurowski, 1992). In rare cases, the height of the lodge surpasses 3 meters. The shape and size of the beaver lodge may change in the course of time due to reconstructing of the lodge for cold season (Zurowski, 1992). Abandoned beaver lodges deteriorate within 2 to 3 years after beaver departures (Zurowski, 1992).

One beaver site, in other words one beaver colony, may contain more than one beaver lodge. It depends on the size of the beaver family and a size of the beaver wetland. One of the lodge in such colony is the main (primary) lodge used for breeding and overwintering while the rests are used as temporary shelters (Дьяков, 1975; Zurowski, 1992). In rare cases, females give birth in secondary lodges (Zurowski, 1992).

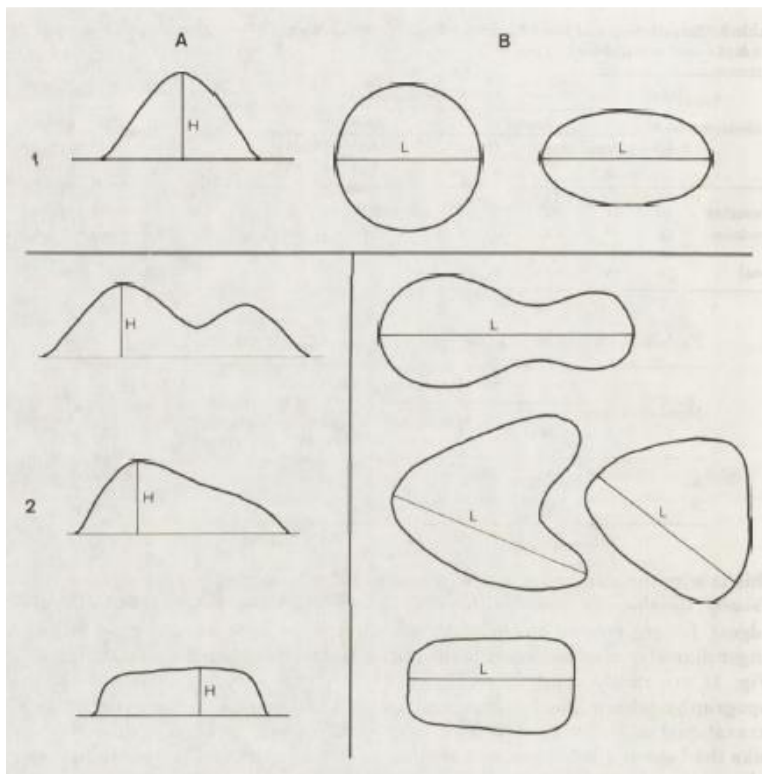


Figure 9. Frequently observed shapes of the beaver lodges. A – side view, B – base view, H – height, L – length. 1 – the most usual conical with circular or oval shape of the base, 2 – other types of lodges (Zurowski, 1992).

The temperature inside the beaver lodge varies less than outside. It never drops below the zero in cold seasons (Stephenson, 1969; Buech *et al.*, 1988; Dyck, MacArthur, 1993). The fluctuation of temperature inside the lodge depends on the activity of the beaver. It decreases slightly, when beavers leaves the lodge. Sometimes in summer, the temperature inside the lodge may be higher than outside. Dyck and MacArthur (1993) have noticed that the temperature is significantly higher in active beaver lodges than in abandoned one in all seasons. The average temperature inside the lodge may depend on the size of the beaver lodge. According to Buech *et al.* (1988), the temperature was higher on average of 7 to 8°C in bigger lodge than in smaller lodges rarely visited by beavers.

In winter, the temperature inside the lodge may be influenced by following factors: 1) the snow cover on the lodge and the body temperature of the beavers (Дежкин, 1959), 2) water temperature (Stephenson, 1969) 3) soil temperature (Buech *et al.*, 1988) and 4) decomposition of organic matter (wood branches and mud). The last factor is less studied. In summer, the temperature inside the lodge is influenced by water (Buech *et al.*, 1988).

Beaver trails and canals. Wherever beavers repeatedly forage away from the water, they carry down vegetation and create trails, especially by dragging tree branches to the water. The trails can be short, merely pathways from the water to solid land. The beavers went farther when food resources are depleted around the pond. Longest recorded trails were in range of 65 to 201 meters (Müller-Schwarze, Sun, 2003).

On the less-level grounds well-worn trails are filled with water, thus beaver canals are made. Beavers further improve these incipient canals by dredging mud

and depositing it at the banks of these canals. The canal eases the transport of logs from the foraging places to the lodge and the dams (Müller-Schwarze, Sun, 2003).

1.3. Impact of beavers to landscape

The effect of Eurasian beaver on the landscape is poorly investigated in Europe (Törnblom *et al.*, 2011) and mainly it included general description of changes happening during construction activities (Sidorovich, 2011), thus the impact on the landscape and habitats will be reviewed using studies of the North American beaver.

The impact of beaver to landscape should be assessed from two aspects: 1) beaver impact to hydrological network after water bodies are formed and 2) impact to surrounding landforms. Due to activities of the beaver, the heterogeneity of the landscape increases significantly (Bogucki, Turner, 1987; Remillard *et al.*, 1987).

Territories affected by beaver are also called beaver sites. A beaver site is defined as a compact territory with beaver buildings like lodges, semi-lodges, burrows, dams, canals and beaver activity signs like food caches, grazing on trees, tracks and trails (Bluzma 2003). Therefore, the beaver site is: 1) the territory flooded by beaver (beaver wetland or beaver ponds) plus 2) the land affected by beavers which boundaries are described by the furthest signs of the beaver activity (Allen, 1982). The relief determines the size of beaver wetland and hydrology (Naiman, Melillo, 1984; Bluzma 2003) while the terrestrial part of the beaver site – mostly by the surrounding vegetation (Allen, 1982).

Beavers build dams in 2nd to 4th order streams (approximately from 1 to 15 meters wide). Dam-building changes the annual stream discharge regime, decreases the current velocity, gives the channel gradient a stair-step profile,

expands the area of flooded soil and increases the retention of sediments and inorganic matter (Naiman *et al.*, 1988). Beavers can influence as much as 30 to 50% of the length of the stream (Johnston, Melillo, 1984). Johnston and Naiman (1990a; 1990c) estimated that North American beaver may alter up to 12% of the suitable landscape in 40 years. Sixty per cent of alterations are newly created water bodies, the other share involves changes in vegetation.

By damming the stream, beaver ponds are created. The size of the beaver pond depends on the width of the river, on the landscape and on the size of the beaver dam (Johnston, Naiman, 1990c). The average beaver pond of North American beaver varies from 3.7 ha to 4.7 ha (Johnston, Naiman, 1990c). The smallest beaver pond of one family could be less than 1 ha, while the biggest up to 45 ha.

Beaver may cause changes in the nutrient cycles in the landscape. When the flow of the river is disturbed, both the organic and mineral matter starts to accumulate in the beaver pond (Hodkinson, 1975; Naiman, Melillo, 1984; Naiman *et al.*, 1986; 1988; Johnston, Naiman, 1987; Ford, Naiman, 1988; Buttler, Malason, 1995, Pollock *et al.*, 1995; Данилов и др., 2007). Different sediment structure and composition are recorded in different locations inside the beaver pond. Decaying wood and plant parts mostly sink in the littoral zone. In the bottom of the pond, sediments and organic matter compose the greatest share. In the parts where winter caches are made, mixed sediments of both plant parts and other organic matter are present (Naiman *et al.*, 1988). The estimated sedimentation rate in beaver ponds varies from 0.26 to 0.6 cm/year (Devito, Dillon, 1993). Due to accumulating organic matter, the beaver pond changes gradually to a shallow beaver wetland and when it is abandoned – to a beaver meadow (Ives, 1942; Naiman *et al.*, 1994; Terwilliger, Pastor 1999; Wright *et al.*, 2002).

1.4. The impact of beaver to plant cover

Beaver impact on the plant communities can be evaluated in two ways: 1) changes in plant community in the flooded habitats and 2) impact on the terrestrial plant community.

Beaver is one of the most significant disturbance factors in the ecosystem (Rossel *et al.*, 2005). By flooding the forest or meadow, new type of habitats and new plant communities are formed. Typical land communities are changed to obligate and facultative wetland plant communitys (Naiman *et al.*, 1986).

After a beaver pond is created, all previous vegetation dies in the newly flooded area of pond. The presence of former forest is indicated by standing dead tree trunks. The terrestrial plant community is changed to an aquatic or riparian plant community (Данилов и др., 2007). Due to high concentration of organic and mineral matter, typical mesotrophic and eutromesothrophic plant communities start to form. Initially free-floating, easily dispersible genera like duckweed (*Lemna* spp.), *Spirodela* spp., watermeal (*Wolffia* spp.) and bladderwort (*Utricularia* spp.) establish in the beaver pond (Ray *et al.*, 2001). Representatives of floating-leaved macrophyte communities (watershield *Brasenia schreberi*, water lily *Nymphaea* spp.) appear last.

Beaver ponds are not permanent elements of the landscape. After the breach of beaver dam or when the beavers leave the pond, it gradually changes to beaver meadows. Hygro- and hygromesophitic community changes to hidrophytic plant community (Simonavičiūtė, Ulevičius, 2007). According to these authors, the species with a wide ecological spectrum can grow in the beaver meadows and the plant community structure does not differ from natural wet meadows that are seasonally flooded. However, eutrophic species are more abundant in beaver meadows than in natural ones.

As mentioned before, beavers are central-place foragers mainly feeding/grazing on plants within 200 m radius around the beaver lodge (Jenkins,

1979; 1980; Данилов и др., 2007). Rosell and others (2005) state that beaver shifts community structure of shoreline vegetation towards non-preferable species. Sometimes the high selectivity of one plant species by beavers may lead to its disappearing from the habitat (Barnes, Mallik, 2001).

North American studies demonstrated, that in alluvial vegetation types, the continuous harvesting of early and mid-successional species by beavers can reverse the progress of succession. After flooding the forest and cutting the trees, open patches are created in the tree canopy, thus secondary succession processes in the habitat are initiated (Johnston, Naiman, 1990b). New environmental conditions, like higher moisture and more sunlight, at the edges of the pond are favorable for *Salix* spp. and *Alnus* spp., which are the main food source for beaver in winter (Nummi, 1989). Beaver also prefers aspen (*Populus* spp.). By cutting aspens, beaver creates unshaded patches in the forest and stimulates the regrowth of adventitious buds by the roots, which sprout around the base of the cut plants (McGintley, Witham, 1985). Young sprouts of aspen are not a favourite food source of beaver, thus in several years new generations of aspens grow in the area.

There are many discussions whether the establishment of beavers in the landscape decreases or increases species richness of plants in the territory. Some studies determined that beaver ponds can support higher (Martinsen *et al.*, 1990; Crooks, 1998) or lower (Bratton, 1975; Collins, Uno, 1983) species diversity in comparison with the non-affected habitats at the local scale. Even the decrease of plant species richness may be significant only in some places at local scale, but at the landscape scale, beavers may significantly increase the plant species richness (Wright, Jones, 2002).

1.5. Eurasian beaver impact on mammals

The effect of beavers on mammals could be discussed by dividing all mammals into ecological groups of carnivores, semi-aquatic, ungulates and small mammals.

Beavers are one available food source for both semi-aquatic and terrestrial carnivores. In particular, beavers are hunted by wolf (*Canis lupus*), brown bear (*Ursus arctos*), red fox (*Vulpes vulpes*), Eurasian lynx (*Lynx lynx*), pine marten (*Martes martes*), American mink (*Mustela vison*) and otter (*Lutra lutra*) (Wilsson, 1971; Djoshkin, Safanov, 1972; Recker, 1977; Dunstone, 1993; Kile *et al.*, 1996; Rosell, Hovde, 1998; Andersone, 1999; Gade-Jørgensen, Stagegaard, 2000; Andersone, Ozoliņš, 2004; Rosell *et al.*, 2005; Sidorovich 2006a; Sidorovich, 2006b, Sidorovich, 2011). Andersone (1999) found that the share of beavers in the wolfs diet may increase due to decreased population size of ungulates. In addition, the season may influence the predation on beaver. Мертц (1953) determined that the share of beavers eaten by wolfs was 5.3% in summer and 15.3% in winter in Voronezh, Russia. According to Sidorovich (2006b), the proportion of beavers in brown bear diet differs among seasons. Sidorovich (2006b) noted, that brown bears hunt on beavers more frequently in early spring and mid-autumn when the chances to catch ungulates are low in northern Belarus. Also, beaver may be an alternative prey for Eurasian lynx, red fox and American mink, thus the proportion in its diet is low (Sidorovich, 2006a), and attacks on beavers are unusual and rare (Kile *et al.*, 1996, Wilsson 1971; Recker, 1977). Wilsson (1971) suggested that only young beavers (1 to 2 months) are probably susceptible to fox attacks while feeding on land before having fully developed escape behaviour. Recker (1977) reported that American mink might hunt on young beavers.

Terrestrial carnivores may use beaver-built structures, like beaver lodges and beaver burrows for various purposes. For example, wolves may widen abandoned and collapsed beaver burrows and use them as temporary shelters

(Барабаш-Никифоров и др., 1961). Sidorovich (2011) determined that polecats use beaver lodges for nesting (breeding and rearing cubs). In addition, polecats, stoats and weasels forage for small mammals and resting in beaver burrows and beaver lodges. Sometimes, when the ceiling of the burrow collapses and the entrance to the burrow is formed, red fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*) and badger (*Meles meles*) may visit or even live in the beaver burrow (Хлебович, 1938; Барабаш-Никифоров и др., 1961).

There is more studies of the relations of beaver with the semi-aquatic mammal species. Sidorovich and others (1996) noted that densities of both otter (*Lutra lutra*) and American mink are increasing with the growth of beaver population western part of Belarusia. Ulevičius and Balčiauskas (1999; 2002) found that the abundance of otter and American mink correlates with abundance of Eurasian beaver in some Lithuanian rivers. Beavers improve habitat for both mustelids that catch pray in the water. American mink and otter may use beaver lodges in winter as the access to unfrozen water (Sidorovich, 2011). Some observations indicate that mink might choose the beaver lodges as their winter home (Zurowski, Kammler, 1987). Mink preys on muskrat (*Ondatra zibethicus*) which sometimes can be abundant in beaver wetlands (Dunstone, 1993). Mink and otter may use abandoned or active beaver lodges, bank dens or holes for shelter, breeding and growing cubs (Sidorovich, 2011). According to Romanowski and others (2013), otter inhabits beaver dens and lodges and hunts in the vicinity of beaver dams.

Small mammals are of great importance as a pray species for American mink (Sidorovich 2011) and less important for otter, and their abundance is generally positively influenced by beaver structures (Ulevičius, Janulaitis 2007; Sidorovich 2011). Amphibians, reptiles, and fish are also positively influenced by beaver impacts (Hägglund, Sjöberg 1999; Balčiauskas *et al.*, 2001; Dalbeck *et al.*, 2007; Башинский, 2008; Sidorovich, 2011). The combination of microhabitats and available food sources suggests high potential of ecological carrying capacity

for American mink and otter in the territories densely inhabited by beavers (Sidorovich, 2011).

Muskrat may be commonly found in beaver wetlands (Knudsen, 1962; Dunstone, 1993). They may use beaver sites more frequently than beaver-free wetlands in the same region (Rutherford, 1955; Knudsen, 1962). In beaver sites, muskrats use food resources and beaver-made microhabitats, like lodges and burrows. Grasse (1951) found that muskrats may also feed on food remains left by beavers; meanwhile according to Tyurnin (1984), they may be using food caches in winter. Leighton (1933) noticed that muskrats might inhabit abandoned beaver lodges.

In analyzing beaver impacts on food resources for muskrat, we must keep in mind not only the support, but also possible competition for certain food categories between these two mammals. For example, beaver and muskrat may compete for *Phragmites* due high preference of this food by both species. However, due to diversity of plant species in beaver sites, the competition is not common between these two species (Дежкин и др., 1986).

The change in composition of woody plant species impacts the distribution of ungulates in the landscape, especially in the cold season. Beaver wetlands attract roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and elk (*Alces alces*) which feed on the bark of willow, aspen, birch (Danilov, 1992; Safonov, Saveljev, 1992), that are more abundant than they were before the beaver settled in the territory. In the warm season, elk feeds on water plants like water lilies (Hilfiker, 1991) and finds cover from biting insects in beaver ponds (Collins *et al.*, 1978; Müller-Schwarze, 1992).

Sometimes relationship between beavers and ungulates may escalate to competition (Язан, 1959; Дьяков, 1975; Hood, Bayley, 2008) which could lead to a decrease in beaver populations (Baker, 2003). Beaver and ungulates, especially elk and moose may compete for the same food resource, mainly – willows (Язан, 1959; Kay, 1994; Baker *et al.*, 2005). Due to high population densities of

ungulates in the territory and intensive foraging on willows, the regrowth of these plant species may decrease which may lead to deficiency of food and building material for beaver. As a result, the density of beavers may decrease (Baker *et al.*, 2005).

Less is known about impact of the beavers on small mammals. According to Medin and Clary (1989) and Suzuki (1992), ecotones of the beaver sites are inhabited by typical wetland species. But due to lack of research, it is hard to conclude whether beaver-transformed habitats attract or deter away small mammals. According to Suzuki and McComb (2004), the capture rates of some small mammals, may be higher in beaver occupied reaches than in unoccupied, while Terwilliger and Pastor (1999) found and opposite results. Suzuki (1992) suggests that after the beavers remove trees and the shores overgrow with grasses, small mammal commonly found in meadows (like *Microtus spp.*) may move in while the forest species abandon the pond edge.

Little is known about the use of beaver-built structures (lodges and burrows) by small mammals. According to Барабаш-Никифоров (1950), more than 20 species of small vertebrates (small mammals, reptiles and amphibians) may be using beaver burrows as shelters. Even though the microclimate of the burrows was not observed in the studies of Барабаш-Никифоров (1950), the author suggested that small vertebrates hide in the beaver burrows from low temperatures. The studies of Ulevičius and Janulaitis (2009) determined that nine species of small mammals used beaver lodges. The core of small mammal community on beaver lodges is composed of bank vole and yellow-necked mouse and common-to-wetlands common shrew. Also they noted, that abundance of bank voles is significantly higher on beaver lodges than in the forest in spring. Authors suggest beaver lodges could for survival of small mammals in winter.

1.6. Helminths of bank vole (*Clethrionomys glareolus*) and yellow-necked mouse (*Apodemus flavicollis*)

According to Mažeika (1992), more than 73 species and taxa of helminths are registered in Lithuania. However, not all helminths are identified up to species level, thus the real number of parasite species is unknown.

The species composition of helminth varies between the host species (Krasnov *et al.*, 2008). Some helminth could be species specific, others could parasitize more than one host. The number of the parasite species depends on the size of the host too (Poulin, Morand, 2000). The bigger the host the greater the number of parasites could be found. The majority of small mammals are final host for helminths (Skorping, Högstedt, 2001).

According to Mažeika (1997), helminths of 42 species parasitize in bank voles. Two out of 42 helminth species of the bank vole are specific to bank vole only: *Heligmosomoides glareoli* and *Syphacia petruszewiczi*. *Hymenolepis horrida*, *Catenotaenia cricetorum*, *Heligmosomum costellatum*, *Syphacia obvelata* are most common helminths in the bank vole. Bank vole is the final host of the tapeworms *Hymenolepis diminuta* and *Rodentolepis straminea*, and the interim host of *Hydatigera taeniaeformis*, which parasitize humans too (Mažeika, 1997). Some individuals of the bank vole could be infected with *Trichinella spiralis* (Prūsaitė, 1988). The species composition of helminth differs between the gender and the season in populations of the bank vole. Male bank voles have the greater number of helminths than females and the infection rate with helminths is greater in winter than in other seasons (Европейская..., 1981).

Helminths of 17 species parasitizes in yellow-necked mice (Mažeika, 1992). The helminths of the yellow-necked mouse are the same as in other mouse species (Prūsaitė, 1988). Yellow-necked mouse is the host of *Hydatigera taeniaeformis*, *Syphacia obvelata*, which can parasitize humans too. The composition of helminths depends on the age, gender and the season in the

yellow-necked mouse. As with the bank vole, males of yellow-necked mouse are more infected than females (Ferrari *et al.*, 2004).

The species diversity and abundance of helminths in small mammal depends on the habitat, where small mammal lives (Голикова, 1960; Abu-Madi *et al.*, 1998, 2000). According to Abu-Madi and others (2000), the infection level of helminth in wood mouse (*Apodemus sylvaticus*) significantly differs between habitats and is lower in wet habitats than in the forest or open areas. Behnke and others (2001) have found that the helminthological status in bank vole may differ between similar forest habitats located in different regions. Therefore, the helminthological status in small mammals is determined more locally than regionally.

2. MATERIAL AND METHODS

2.1. Study area

This research on the impact to habitat structure by Eurasian beaver activity and the significance of this impact to other mammal species was carried out in the Vilnius, Molėtai and Širvintos districts in eastern Lithuania at two research plots (Fig. 10). The hilly morainic landscapes is common to the region with average forest cover of 28% (GIS analysis). Norway spruce (*Picea abies*), downy birch (*Betula pubescens*) and alders (*Alnus* spp.) form the core of the forest stands. Numerous abandoned successive meadows, fragments of woodlands from 0.1 ha to 6500 ha, and various types of wetlands contribute to the structural mosaic of the landscape.

Up to 40% of the landscape is composed of positive forms of relief in the form of hills. Various types of water bodies and wetlands, overgrown with willows and grey alder, have formed in depressions between the hills in the lowlands, which occupy up to 30% of the landscape (Basalykas, 1977). These wetlands are highly preferred by Eurasian beavers. According to previous studies by Bluzma (2003) and Ulevičius (2008), the density of beaver sites in the territory was 19 beaver sites/1000 ha.

The study of the significance of the Eurasian beaver to semiaquatic mammals was carried out in 69 river fragments across Lithuania (see Fig. 12 in paragraph 2.5. and Annex 1). The research grid covered the area of Lithuania evenly. Signs of semi-aquatic mammals were studied both in fast- and slow-flowing, and in straightened rivers with sandy beaches, alluvial sites.

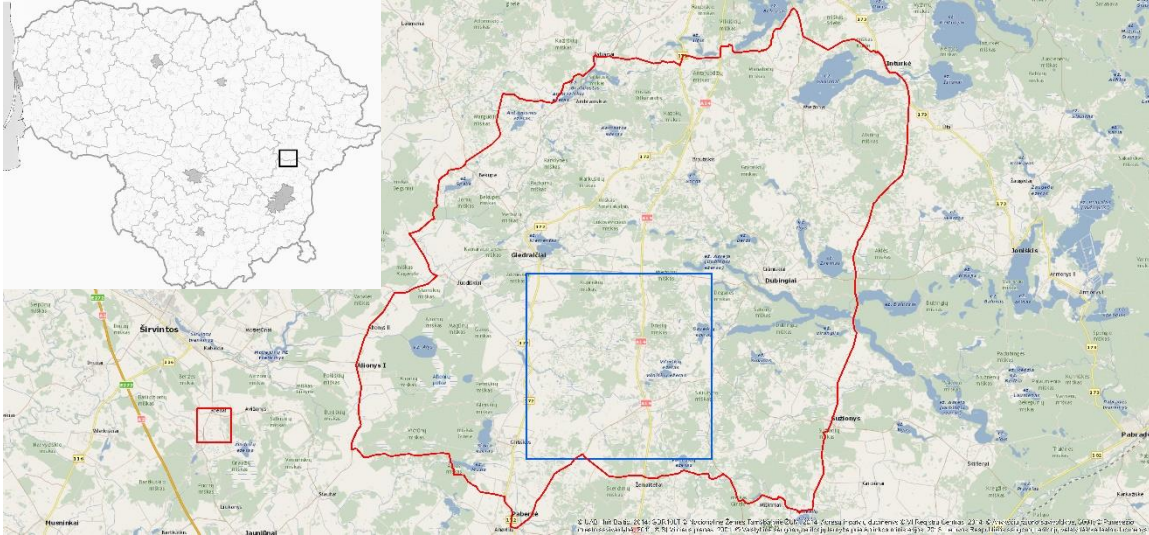


Figure 10. Study area in eastern Lithuania. Two study plots are indicated by red outlines. The territory where the evaluation of Eurasian beaver impact to habitat structure was carried out is marked with blue outline.

2.2. Evaluation of Eurasian beaver impact to habitat structure

Studies were carried out in 100 km² plot in the eastern part of Lithuania, in Vilnius and Molėtai districts (Fig. 10).

The evaluation of the habitats in the territory was performed using GIS ESRI®, ArcGIS 10.x.® and the orthophotos of Lithuania (1: 10 000, GDR10LT (2009-2010), National Land Service under the Ministry of Agriculture). Nine habitat categories were identified: open areas, forests, lakes, rivers, drainage ditches, swamps, beaver wetlands and beaver sites, and ecotones. Spatial measurements of habitats (area, perimeter, drainage ditch density, ecotone lengths) were derived from orthophoto base of Lithuania.

Beaver impact to habitat structure was evaluated by measuring area and ecotone length, plant cover of beaver wetlands and beaver sites and consecutive comparison with corresponding parameters of other habitats.

The beaver site is an area that consists of beaver wetland and adjacent terrestrial habitats that were affected by beaver (terrestrial activity) and can be delineated by joining the most extreme points of beaver activity (mostly tree cuttings or points of beaver burrow collapses). The beaver wetland is a discrete area with visible beaver engineering activities including beaver lodges, beaver dams, beaver burrows and beaver pathways and canals. Post-engineering effects include beaver ponds and inundated with water forests, after the beaver dam is built, with standing dead woods, and beaver feeding activity associated with cut trees.

The area of a beaver site could not be marked on a map directly because the canopy of the forest hid most of the marks of the beaver activities. This detection bias could result in area estimation errors. Therefore, measurements *in situ* were made to evaluate this error and correctly digitize beaver sites on the orthophotos. The research was conducted in two phases.

First, the area of a beaver wetlands was estimated with GIS ESRI®, ArcGIS 10.x.®. This measure was called an *ex situ* beaver wetland. Selected *ex situ* beaver wetlands ($n=15$) were measured in the field (*in situ*) to minimize digitization errors when using the orthophoto by applying a correction coefficient (see paragraph 2.3.1). This correction coefficient derived from comparison between *ex situ* and *in situ* measurements of the selected beaver wetlands ($n=15$).

The *in situ* measurements were carried out at 15 beaver wetlands from 2011 to 2015 in winter and spring seasons using a high proximity tool „Trimble® GPS Pathfinder® Pro Series“ with accuracy of 50 cm. The coordinates of water margin were taken every 5 to 10 meters. The coordinates were transferred to the GIS ESRI®, ArcGIS 10.x.® and connected to form the polygons. The *in situ* measured wetlands were compared with corresponding *ex situ* wetlands. Non-parametric Wilcoxon test was used for testing the differences (Gotelli, Ellison, 2013).

Second, the terrestrial activity of beaver activity was measured in the fields. The coordinates of beaver activity were taken and signs like beaver dams, collapsed beaver burrows and cuttings were documented. Beaver cuttings were identified to genus or species level. The coordinates were transferred to the GIS ESRI®, ArcGIS 10.x.® and analyzed to find the average distance to beaver terrestrial activity from the shore.

Studies of plant cover types were carried out at 15 beaver sites *in situ*. Seven categories of plant cover were described: 1) sedges, 2) shrubs, 3) reeds and bulrushes, 4) swampy forest, 5) snag stands, 6) horsetail beds and 7) *Sphagnum* spp. mets. Specific areas of the beaver sites were assigned to one of the cover type if the projection of canopy of one plant species/genus exceeded 50% of total canopy area. The area of plant cover was estimated with ESRI®, ArcGIS 10.x.® and the orthophotos of Lithuania (1: 10 000, GDR10LT (2009-2010), National Land Service under the Ministry of Agriculture).

2.3. Validation of the GIS method

2.3.1. Correction coefficients for wetlands

1st correction coefficient. We have found that beaver wetlands *in situ* were significantly larger in area than the same *ex situ* wetlands (Table 1) from 1.26% up to 200% with an average of $30.95\% \pm 33.58$ (SD). The smaller the *ex situ* wetland was, the larger was the differences in size between the *ex situ* and *in situ* wetland (Spearman rs; $p=0.05$). This finding indicates that *ex situ* analysis of smaller beaver wetlands resulted in higher underestimations. The first correction coefficient for estimation of beaver impact to landscape was 1.3, which indicated that the size of beaver wetland measured *in situ* was 1.3-fold larger than the measured *ex situ* wetland.

2nd correction coefficient. To minimize the effect of digitizing errors (Berry, Berry, 1988; Bone and Johnson, 2007), which could occur when orthophotos were digitized, and to lower the standard deviation we removed one wetland with the lowest and one wetland with the highest *in situ* : *ex situ* ratio. Thereafter, we found that the *in situ* wetlands were larger in area than *ex situ* by an average of $21\% \pm 14.7\%$ (SD) (Wilcoxon test; $p < 0.001$). Thus the second correction coefficient was 1.2, which indicated that the size of beaver wetland measured *in situ* was 1.2-fold larger than the measured *ex situ* wetland.

After correction of the *ex situ* wetlands with two different correction coefficients, we determined that the size of all corrected *ex situ* wetlands did not differ from the *in situ* wetlands (Table 1). Thus, all corrections could be used to estimate the real size of wetlands in the orthophotos. For later studies, we used only the 2nd correction coefficient, to multiply the area of *ex situ* wetlands by 1.2.

The 2nd correction coefficient was chosen for two reasons: 1) reduction of digitizing error, which occurs digitizing the orthophotos, and 2) the area of *ex situ* wetlands corrected with this coefficient significantly differed from the area of *ex situ* wetlands corrected with the other coefficient.

Table 1. Differences (Wilcoxon test, p) between the *ex situ* and the *in situ* estimates of beaver wetlands. Areas of wetlands of *ex situ*, *in situ*, *ex situ* corrected by 1.2 (C 1.2), *ex situ* corrected by 1.3 (C 1.3)

Wilcoxon test	<i>in situ</i>	C 1.2	C 1.3
<i>ex situ</i>	0.007	0.002	0.005
<i>in situ</i>		0.9	0.16
C 1.2			<0.001

2.3.2. Correction coefficient for terrestrial part of the beaver site

A very important factor determining the area of the forest affected by Eurasian beaver was the composition of the surrounding vegetation. We found

that the farthest distance any tree grazed by Eurasian beaver was 51 meters from the shore. Aspen (*Populus tremula*) was the farthest plant grazed by beaver. Also, at all beaver sites where aspen was abundant all aspen trees were cut up to 50 meters from the shore. Willows (*Salix* spp.) were taken the second farthest from the shore (48 meters). Smaller distances from the shore to the grazing were observed for spruce (*Picea abies*) (43 m) and for common hazel (*Corylus avellana*) (24 m). It must be emphasized that the spruce cut by beavers was very young and it was cut at only one beaver site where the density of spruce was very low. Spruce trees were not cut at other beaver sites, where they were more abundant and older. We found that birches and oaks were never cut more than 10 meters from the shore.

The second factor, we found to be important, was the type of the beaver wetland (Table 2). Although the plant species composition was similar at all beaver sites we found that the average distance to the beaver sign statistically differed between the various types of the wetlands (Kruskal-Wallis: $p=0.02$). Beavers travel the greatest distance from the edge of water (shore) to forage species at sites with open water and travel the least in reed and sedge swamps. The same tendency was visible in the average farthest distance (Kruskal-Wallis: $p = 0.06$).

Table 2. The farthest and average distance (m) from the shore to the beaver sign in different type of beaver sites.

Beaver site type	n	Fartherst	Average
Open water	5	49.17	12.56
Reed and sedge	3	33.77	2.17
Shrubby	7	51.3	8.46

We determined two correction coefficients to estimate the minimal and the maximum effect of the Eurasian beaver to the terrestrial part of the beaver site in the study area. The minimal effect of the Eurasian beaver to the forest was

evaluated by calculating the area of the forest in a radius of 12.5 m around beaver wetlands with open water, in a radius of 2 meters around beaver wetlands with reed and sedge and in in a radius of 8.5 m around the shrubby beaver wetlands. These coefficients are the equivalent to average distance from the shore to the beaver sign in different type of beaver sites. The maximum area of the forest habitat affected by Eurasian beaver was estimated by calculating the area of the forest in a radius of 51 m from the edge of the beaver wetland. This is the equivalent to the farthest beaver sign that was found in the study area.

2.4. The significance of Eurasian beaver-modified habitats to mammals of different ecological groups

In the study area, we randomly sampled 55 plots of 1 km² (Fig. 11). The randomly generated plots were transferred on the gridded study area map using ESRI®, ArcGIS 10.x®, with the conditions that plots cannot contact each other either with the sides or with the corners. If these conditions were violated, the plot was moved to closest cell in any direction avoiding the contact with other plots.

Elements of the landscape in every plot were evaluated using ESRI®, ArcGIS10.x®. Landscape diversity index was calculated for every plot. Natural logarithm was used for diversity estimation.

Research on animal abundance indices was conducted out in 1 km² plots in winters of 2013 and 2015. Animal tracks were counted along 1 kilometre long transects. We checked total of 57 transects (some of them were checked twice but in different years). When a transect was placed in the plot, it had to cross all the existing habitats and the share of the habitats in the plot had to be reflected in the transect. The abundance index was defined as the number of tracks that crossed the transect line per 100 meters per day without snowing (Balčiauskas, 2009).

Tracks were identified to genus or species level. Because it is difficult to distinguish tracks of certain Mustelid species from each other, pine marten

(*Martes martes*) and beech marten (*Martes foina*), were grouped as *Martes* sp., while tracks of least weasel (*Mustela nivalis*) and stoat (*Mustela erminea*) were grouped as *Mustela* sp.

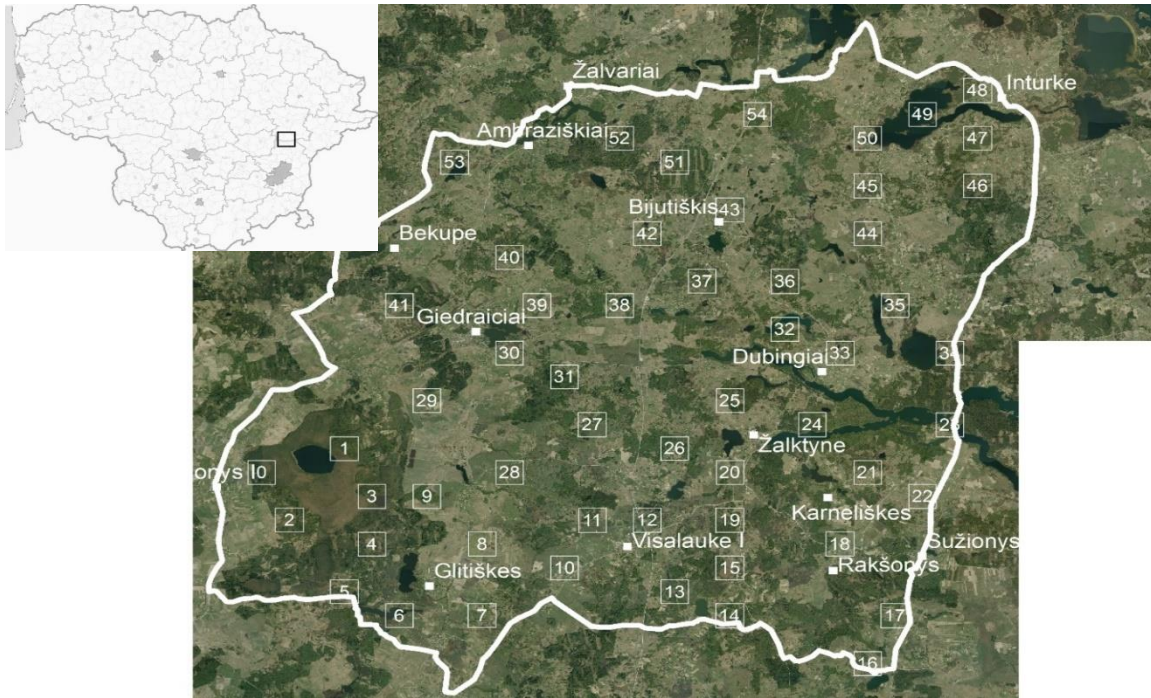


Figure 11. Study area with 55 plots of 1 km² in which the research on mammal tracks was carried out.

To estimate the importance of habitats transformed by Eurasian beaver to other mammals, the length of the beaver wetland ecotone, the area of the beaver site and the diversity index of the landscape were compared with the abundance index of mammal tracks. Linear correlation was used to evaluate the dependency (alpha $p=0.05$) (Gotelli, Ellison, 2013). Shannon's diversity index with logarithm base of 2 was used to evaluate landscape diversity in every plot (Poole, 1974). A Kurskal – Wallis test was used to estimate differences of abundance indices between species and habitats (alpha $p=0.05$) (Dytham, 2001).

Additional research was performed to estimate the attractiveness to mammals of habitats inside the plot. Four habitats were distinguished: forest, beaver wetland (all wetlands in the research plots were occupied by beaver), meadows and mosaic. Mosaic is defined as habitat, where fragments of forests and wetlands of different size are interfered in meadows.

Research on American mink (*Neovison vison*) was carried out in beaver wetlands in winter from 2009 to 2011 and in 2013 and 2014. No study was done in winter of 2012. A total of 181 beaver wetlands were observed during the research period. The absence or presence of American mink was recorded in each beaver site. Activity signs like tracks and faeces of American mink were recorded. The frequency of occurrence (FO) of species was calculated by the principle of present or absent in one transect. Percentages were used to express this dimension. A chi-square goodness-of-fit test was used to evaluate the differences of frequency of occurrence between the years ($\alpha p=0.05$).

2.5. The study of the significance of Eurasian beaver abundance on semi-aquatic mammals in rivers of Lithuania

In spring and summer of 2012 and 2013 a total of 69 river fragments were studied across Lithuania (Fig. 12). Signs, such as tracks, pathways, feces and marking piles of semi-aquatic mammals were observed in one kilometer long segments of the river shoreline. The abundance index of signs per 1 kilometer of the river segment was used to evaluate density of semi-aquatic mammals.

T test was used to compare the abundance indices of semi-aquatic mammals ($\alpha p=0.05$).



Figure 12. The research network on abundance of semi-aquatic mammals in rivers of Lithuania (number indicates the approximate location of the studied segment and the river name that is given in Annex 1)

2.6. Sampling of small mammals

Small mammals abundance on beaver lodges and in the control habitats of the forest were sampled by setting a quadrat of five snap traps (one in the middle of the quadrat and four in the corners approximately 5x5 meters) both in the forest and on the beaver lodges (Fig. 13). Standard sampling method, the line of 25 snap traps, could not be used due to small size of beaver lodge as a habitat. In winter, when thick snow cover was present, snap traps were placed on bare ground after snow was removed from the ground, thus, forming holes of about 0.5 m diameter around a trap. On beaver lodges, the central trap was usually placed on top of a lodge and the other four traps – around the base of a lodge. Small mammals were sampled at beaver sites and in the forest from 2007 to 2011 four times per year: in spring (April), in summer (August), in autumn (October) and in winter (February).

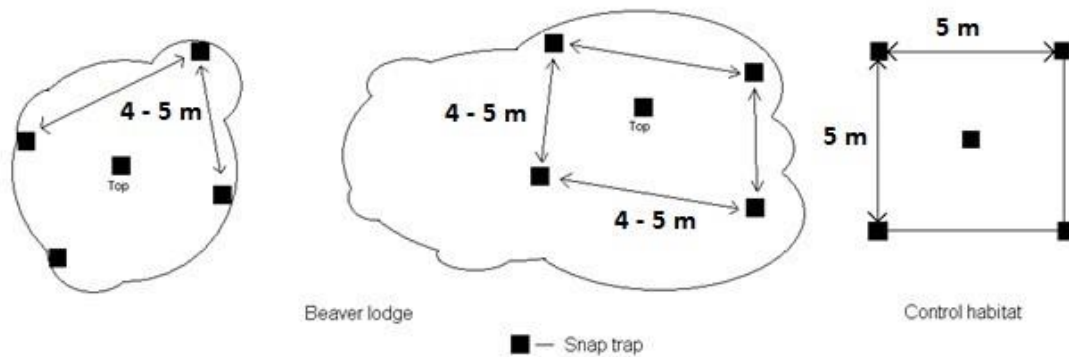


Figure 13. Snap trap placing schema on beaver lodges and in the control habitat of the forest.

There were 2700 snap trap nights on beaver lodges and 2250 snap trap nights in the forest. We captured 492 small mammals on beaver lodges and 238 small mammals in the forest. Data on trapping efforts, captures, habitat and season are presented in Table 3.

Table 3. Trapping effort, the total number of small mammals and number of species caught on beaver lodges (BL) and in the forest (F) during different seasons from 2007 to 2011.

Indicator	Spring		Summer		Autumn		Winter		Total	
	BL	F	BL	F	BL	F	BL	F	BL	F
n*	44	39	47	39	47	39	42	33	180	150
Trapping effort, trap-nights	660	585	705	585	705	585	630	495	2700	2250
Number of small mammal caught	49	32	150	85	218	102	75	19	492	238
Number of small mammal species identified	5	3	9	3	10	4	5	3	11	4

* n – number of studied beaver lodges and forests studied

In the study, small pieces of brown bread crust moistened with sunflower oil were used as bait. Traps were set for three days and checked once a day.

Sampling during three days was defined as one trapping event and considered as one element of a sample. Sampling of small mammals by snap traps was permitted by the Ministry of Environment (license No. (11-)-D8-3650).

Captured small mammals were identified up to species level. The identification of *Microtus* sp. was performed in laboratory where differences of dental morphology were analyzed (Niethammer, Krapp, 1982; Prūsaitė, 1988).

Trapped bank voles were grouped by sex and age and individuals were divided into three age groups: juveniles, sub adults and adults. All pregnant females and females with visible signs of previous pregnancy and males with scrotal testes were defined as adults. All individuals without developed reproductive organs were assigned as juveniles. All other small mammals were assigned to sub adults. The presence and status of *glandula thymus*, as well as the weight of an individual were taken into account when determining the age (Prūsaitė, 1988; Balčiauskas, Gudaitė, 2006).

The number of small mammals caught on beaver lodges and in control habitat of the forest was expressed as trapping success (TS) and defined as the number of animals caught per 100 trap nights. A Shannon-Weaver biodiversity index (with logarithm base 2) was used to estimate small mammal diversity in different habitats (Shannon, Weaver, 1949). Data on trapping success in the majority of samples failed the normality test (Shapiro-Wilks test: alpha $p=0.05$), thus, significance of differences in trap success of small mammals was tested using the nonparametric Mann-Whitney and Kruskal-Wallis tests for pairwise and multiple comparisons, respectively (Gotelli, Ellison, 2013).

The structure of the small mammal community was determined by comparing the percentage contribution of each species or species group to the total mammal community. The most abundant four species of small mammals (bank vole, common shrew, yellow-necked mouse and short-tailed vole) were analyzed as separate contributors to the community structure, whereas the rest of rarely

occurring species were pooled together (“other species”). Seasonal differences in community structure were tested using the Yates’ χ^2 test (alpha $p=0.05$).

Frequency of occurrence (FO) of small mammals was expressed as proportion of positive catching events. A trapping event was considered to be positive to a species when at least one specimen of this species was caught per three trap nights.

2.7. Camera traps

We used *Reconyx PC800 HyperFire Professional Semi-Covert IR* cameras with the following basic technical specifications: trigger speed – 0.2 sec; image data – time, date, temperature and Moon phase; IR flash range – up to 21 m; battery life – up to 40 000 images; image resolution – 3.1 Mp or 1080P HD; operating temperature: -40° to $+60^{\circ}$ C.

An original platform was designed to mount a camera (Fig. 14). The frame of this platform was made with a steel-mounting skeleton and the camera was attached to a wooden plate by a self-fastening zip-tie. Two legs penetrating into the beaver burrow’s floor allowed the camera to be set in the desired position.

To install a camera, we searched for a beaver burrow with a complex configuration (i.e., connected to a whole burrow system) and enough internal space in which to place a camera. Then the direction and extent of a burrow cavity was tested using a steel rod. Once an appropriate burrow was found, a hole was made in a burrow’s ceiling, which created an opening into the burrow, thereby allowing us to install the camera. Through this hole we evaluated slope and exact direction of a burrow cavity towards entrance and then fixed an activated camera. Finally, the hole was carefully repaired using strong wooden sticks and debris, which left the set camera embedded in the burrow tunnel. Activated cameras were left in beaver burrows from 30 to 117 days.



Figure 14. Camera fixed on the platform ready to be installed into a beaver burrow (photo by A. Ulevičius).

Beaver sites, in which the camera traps were installed, were classified into the three habitat categories:

1. rivers – natural water streams with a water yield more than 5 m³ per second; beavers burrow in the river banks; significant fluctuations of the water level; no beaver dams;
2. drainage ditches – artificial water streams with a water yield less than 0.5 m³ per second; beavers burrow in the canal slopes; moderate fluctuations of the water level; strong beaver damming activity;
3. wetlands – extensive swampy areas as a result of beaver activities; beavers burrow in steeper slopes on wetland margins.

Trapping events (a camera trap active in a burrow for a specific time period) were grouped by two seasons: 1) warm season – from April to October with mean of +10.6°C and 2) cold season – from November to March with mean of -0.8°C.

A total of 37 beaver burrows were investigated. The distribution of studied beaver burrows among the habitats and seasons is provided in Table 4.

Table 4. Sample sizes of the study beaver burrows in different type of habitats and seasons.

Habitat	Warm season		Cold season	
	Number of burrows studied (catching events)	Number of effective triggers	Number of burrows studied (catching events)	Number of effective triggers
River	4	102	5	1602
Drainage ditch	5	447	9	1272
Wetland	7	875	7	2394
Total	16	1424	21	5268

We used definition of effective trigger as a camera activation event resulting in an animal photo that allowed species recognition (or other taxa) of the animal that activated the camera. Once a camera was activated, it produced 3 to 5 photos per one trigger to enhance probability of catching an animal. Consequently, if an animal was not recognizable from these photos, it was classified as an ineffective trigger. Ineffective triggers were activated not only by mammals, but also by other moving objects (falling ground and drops of water, spiders, moving roots, etc.). In results, we used a term “**Visiting intensity**” (VI), which means the number of effective triggers per 30 days. It is a standardized indicator for estimates of use of beaver burrows among species.

We counted only those effective triggers that were separated by time intervals not shorter than 5 minutes for the same animal species. Time intervals were not taken into account when successive effective triggers were activated by different animal species.

For the 24-hour activity comparison between cold and warm seasons, the day was divided in two periods: first period of dark and second – of light. In cold season, the period of darkness lasted from 17:00 to 08:00 and the period of light –

from 08:00 to 17:00. In warm season, the period of darkness lasted from 22:00 to 06:00 and the period of light – from 06:00 to 22:00

2.8. Helminthological studies

The helminthological status of the bank vole and the yellow-necked mouse was studied at beaver sites and in the control habitat of the forest. The sample sizes are given in the Table 5.

Table 5. The number of bank vole (*Clethrionomys glareolus*) and yellow-necked mouse (*Apodemus flavicollis*), used for helminthological studies in beaver sites and in the forest in different seasons.

Habitat	Spring	Summer	Autumn	Winter	Total
<i>Clethrionomys glareolus</i>					
Beaver site	23	26	66	16	131
Forest	22	43	80	14	159
<i>Apodemus flavicollis</i>					
Beaver site	3	8	10	0	21
Forest	12	18	46	6	82

For helminthological studies, the entire intestinal tract of small rodents was dissected. The content of the intestines was studied by the method of consistent flushing. The helminths were fixed in 70% ethanol. Nematodes and trematodes were studied using temporary water-glycerin preparation.

Two indices of infection level were used. Mean abundancy is the total number of individuals of particular parasite species in a sample of particular host species divided by the total number of that species examined (Bush *et al.*, 1997). The prevalence of infection was calculated as the percentage of the infected individuals among all dissected rodents (Bush *et al.*, 1997). Significance of differences in mean abundance and prevalence of infection was tested using the

Mann-Whitney U test and the chi-square goodness-of-fit test, respectively (alpha $p=0.05$).

The diversity of helminth in small mammals was estimated with Shannon's diversity index with natural logarithm. The domination of helminthes was evaluated with Berger-Parker dominance test (May, 1975).

3. RESULTS

3.1. The ecological impact of the Eurasian beaver on habitat structure a landscape level

After evaluating the 10,000 hectare study area in eastern Lithuania using GIS, we found that the density of the beaver sites was 26.1 beaver sites per 1000 hectare. The signs of Eurasian beaver were found in 87% of the wetland habitats, which is 78% of total wetland area in the study area (Table 6).

By creating new ponds and maintaining beaver wetlands, beavers create new habitat types in the landscape. We determined that the Eurasian beaver in the study area affected more than 26% of the length of all ecotones (Table 6). Only the length of ecotone of forest/open area was longer than beaver-affected ecotones.

Table 6. Extent of beaver impact to habitat structure in a study area (10, 000 ha) in eastern Lithuania.

Cover or ecotone type	Cover area, ha Ecotone length, km	%
<i>Cover type</i>		
Open area	6290	62.9
Forest	2892	28.92
Wetlands created or maintained by beavers	565	5.65
Wetlands without signs of beavers	151	1.51
Other	102	1.02
Σ	10 000	100
<i>Ecotone type</i>		
Forest/open area	559.45	60
Beaver wetland/open area	134.6	14.4
Beaver wetland/forest	110.85	11.9
Other wetland/open area	49.74	5.2
Other wetland/forest	29.24	3
Other	29.06	3
Beaver pond/open area	17.93	1.9
Beaver pond/forest	5.62	0.6
Σ	933.04	100

The larger the wetland the higher the probability of finding beaver signs in wetland. More than 70% of wetlands that were greater than 1 ha were occupied by Eurasian beaver, while 84% of wetlands smaller than 1 ha were vacant (Fig. 15). This finding indicates that the Eurasian beaver prefers wetlands that are greater than 1 ha in size (χ^2 test: $df = 1, p < 0.01$). The smallest wetland with observed beaver sign was 0.097 ha in size.

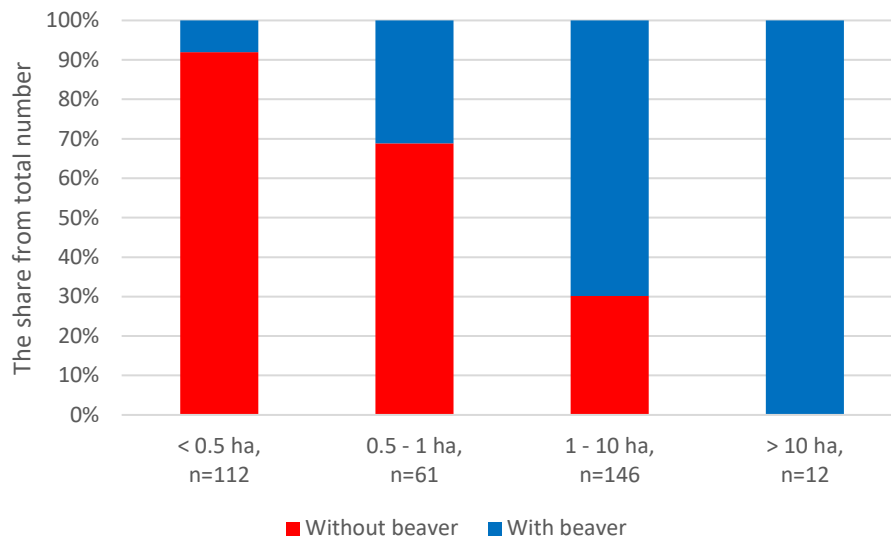


Figure 15. Ratio of different size of wetlands with and without Eurasian beaver in study area.

The variety of beaver sites of different ages may increase the heterogeneity of the habitat structure in the landscape. The uneven overgrowth ration of the beaver wetland with water plants (nymphheids and helophytes) and shrubs was observed in the beaver sites of different ages. This ratio ranged from 0.05 to almost 0.6. The younger the beaver site was, the higher the overgrowth ratio was (Fig. 16), which means, the older the beaver site was, a larger area of water surface was covered with water plants or shrubs (Spearman's $r_s: p = 0.0004$).

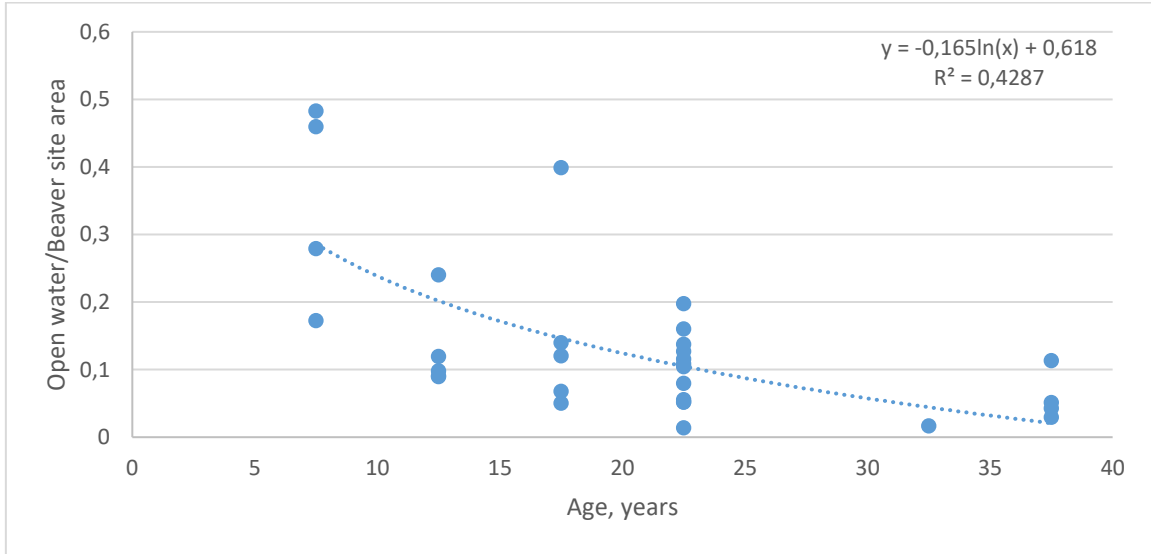


Figure 16. The correlation of age of beaver site and the ratio of open water/beaver site area in study area.

Seven cover types of plant cover were distinguished in beaver sites (Table 7). Three cover types (sedge cover, shrub cover and reed and bulrush beds) were more common to beaver sites than other types. Sedges were the most frequent plant cover type in beaver sites and covered more than 42% of the area beaver sites in the study. Shrubs and reed and bulrush beds were also common vegetation types at beaver sites (73.3%) but the area covered by these plants was significantly smaller than the area covered by sedges (Mann-Whitney: $p < 0.05$). Swampy forest and snag stands together comprised more than half of beaver sites in the study but also the area covered by these habitats was significantly smaller than the area covered by sedges (Mann-Whitney: $p < 0.05$)

Table 7. The average area covered by specific plant cover types and the frequency of occurrence of these cover types in beaver wetlands (BW) ($n=15$).

Cover type	Mean area of coverage/BW, ha	Share in total coverage of BW, %	Frequency of occurrence, %
Sedge cover	1.31	42.4	86.7
Shrub cover (mainly <i>Salix</i> spp)	0.48	17.8	73.3
Reed and bulrush beds	0.45	17.6	73.3
Swampy forest	0.31	10.1	46.7
Snag stands	0.21	6.9	26.7
Horsetail beds	0.19	6.3	33.3
<i>Sphagnum</i> spp. carpets	0.12	4.0	6.7

Additionally, beavers modified 21% of the drainage of field and near-to-forest channel network. We found an average of 0.6 beaver dams per 1 kilometer of the drainage ditch. Beaver ponds varied in size from 2.6 m² to 69 m². The total area of beaver ponds was 8.91 ha (0.089% of the study area).

Different evaluation methods revealed different impacts of the Eurasian beaver on the landscape (Table 8). Using “*ex situ* only“ methods, the evaluated impact of the Eurasian beaver was 2 to 2.5 times less than when impacts were evaluated with applied corrections. The “*ex situ* only“ method does not allow us to estimate the true size of beaver wetlands and the impact of the Eurasian beaver to terrestrial habitats. Final evaluation of the impact of the Eurasian beaver on the landscape and habitat structure indicates that the area affected by the Eurasian beaver was between 9 to 12.4% of the total study area (Table 8).

Table 8. Evaluation of impacts of the Eurasian beaver to the study area of 100 km² with two methods - *ex situ* only and with applied corrections.

Beaver habitat	<i>Ex situ</i> only	Corrected
Beaver wetland, km ²	5.65	7.59
Forrest affected by beaver, km ²	-	1.34 to 4.72
Beaver ponds, km ²	0.1	0.12
Total impact of beaver, km²	5.75	9.05 to 12.43

3.2. Significance of Eurasian beaver-modified habitats to mammals of different ecological groups

3.2.1. Significance of Eurasian beaver-modified habitats to ungulates, lagomorphs and carnivores

Tracks of 13 taxa were identified during the study period (Table 9). The highest abundance indices were found for roe deer, red fox and European hare in all plots and in the different habitats. The abundance index of dominant roe deer differed between the habitats (Kruskal-Wallis: $p = 0.03$). *Post hoc* analysis showed no statistically significant differences for the abundance index of roe deer between the beaver wetland, forest and mosaic habitats. However, statistically significant differences were found between the meadows and other habitats (Mann-Whitney: $p < 0.05$). The mean abundance index of subdominant species of red fox (Kruskal-Wallis: $p = 0.32$) and European hare (Kruskal-Wallis: $p = 0.27$) did not differ significantly between the habitats. The total abundance index of all mammals significantly differed between the habitats (Kruskal-Wallis: $p < 0.001$).

Although we did not find a statistically significant preferences of animals for beaver wetlands in comparison with other habitats, there was a tendency for a higher abundance index for elk and red fox was observed in beaver wetlands (Table 9).

Table 9. The average abundance index (tracks per 100 meter) and standard deviation of mammals in study area and in different habitats.

Species	In the study area	Beaver wetland	Forest	Meadow	Mosaic
	n=57	n=13	n=31	n=32	n=10
<i>Capreolus capreolus</i>	0.88 ± 0.89	1.12 ± 1.49	1.15 ± 1.05	0.45 ± 0.58	0.9 ± 1.2
<i>Vulpes vulpes</i>	0.44 ± 0.37	1 ± 1.17	0.44 ± 0.57	0.52 ± 0.54	0.37 ± 0.30
<i>Lepus europaeus</i>	0.3 ± 0.41	0.3 ± 0.57	0.3 ± 0.47	0.53 ± 0.71	0.22 ± 0.26
<i>Sus scrofa</i>	0.15 ± 0.29	0.01 ± 0.04	0.39 ± 0.79	0.06 ± 0.22	0.01 ± 0.02
<i>Martes</i> sp.	0.15 ± 0.26	0.35 ± 0.75	0.32 ± 0.43	0.05 ± 0.18	0.12 ± 0.19
<i>Mustela</i> sp.	0.12 ± 0.29	0.09 ± 0.3	0.02 ± 0.09	0.13 ± 0.38	0.1 ± 0.2
<i>Alces alces</i>	0.1 ± 0.32	0.36 ± 1.17	0.06 ± 0.15	0.06 ± 0.16	0.24 ± 0.67
<i>Cervus elaphus</i>	0.04 ± 0.16	0.03 ± 0.07	0.04 ± 0.13	0	0.12 ± 0.35
<i>Sciurus vulgaris</i>	0.03 ± 0.016	0	0.06 ± 0.22	0	0
<i>Nyctereotes procyonoides</i>	0.02 ± 0.06	0	0.04 ± 0.13	0.004 ± 0.02	0.04 ± 0.11
<i>Neovison vison</i>	0.02 ± 0.05	0.03 ± 0.08	0.01 ± 0.02	0.02 ± 0.09	0.05 ± 0.09
<i>Lutra lutra</i>	0.01 ± 0.04	0	0	0.004 ± 0.02	0
<i>Mustela putorius</i>	0.001 ± 0.02	0	0.01 ± 0.05	0	0
Total:	2.99 ± 2.49	3.38 ± 2.41	2.85 ± 1.52	1.83 ± 1.08	2.16 ± 1.29
Shannon's diversity index	2.7	2.351	2.551	2.378	2.581
For ecological groups					
Ungulates	1.17 ± 0.95	1.61 ± 1.88	1.64 ± 1.28	0.58 ± 0.67	1.27 ± 1.26
Carnivores	0.76 ± 0.59	1.46 ± 1.64	0.85 ± 0.82	0.72 ± 0.67	0.68 ± 0.48

After comparing the plots with and without Eurasian beaver, we found that the plots with beaver wetlands ($n = 48$) had a greater total abundance index of mammals than those where beaver wetlands were absent ($n = 9$), but the differences were not statistically significant (Mann-Whitney test: $p = 0.09$) (Table 10). The presence or absence of beaver wetlands in the territory were more important for elk than for other species. No tracks of elk were found in plots without beaver wetlands and elk were present in 39% of the observed beaver wetlands. However, no significant differences were found between plots with and without beaver wetlands (χ^2 test: $df = 1$, $p = 0.09$). In addition, there were no significant differences in the abundance indices of mammals between the plots where the total area of the beaver wetland was ≤ 10 ha versus plots where the wetland was > 10 ha.

Table 10. The effect of the presence of the beaver in the study area of 1 km² on the average abundance index (AI) and frequency of occurrence (FO) of mammals (significant differences are bolded)

Ecological group/ species of mammals	Presents of beaver site in the plot	Average AI	SD	Mann-Whitney, <i>p</i>	FO, %
All mammals	Yes (n=48)	2.38	1.33	0.09	97.96
	No (=9)	1.60	1.11		100.00
Ungulates	Yes (n=48)	1.27	0.98	0.04	91.84
	No (=9)	0.59	0.56		88.89
Carnivores	Yes (n=48)	0.77	0.61	0.97	95.92
	No (=9)	0.71	0.48		100.00
<i>Capreolus capreolus</i>	Yes (n=48)	0.95	0.94	0.13	89.80
	No (=9)	0.48	0.40		88.89
<i>Vulpes vulpes</i>	Yes (n=48)	0.46	0.39	0.86	95.92
	No (=9)	0.36	0.23		100.00
<i>Lepus europeus</i>	Yes (n=48)	0.33	0.43	0.21	75.51
	No (=9)	0.16	0.23		44.44
<i>Alces alces</i>	Yes (n=48)	0.12	0.35	0.03	38.78
	No (=9)	0.00	0.00		0.00

2.2.2. Abundance of semi-aquatic mammals in rivers affected by Eurasian beaver

Our research documents that the Eurasian beaver is the most abundant semi-aquatic mammal in rivers in Lithuania (Table 11). Signs of Eurasian beaver activity were found in all studied segments of rivers. Otter and water vole were the subdominant semi-aquatic species found in the rivers (66% and 50%, respectively). The rarest species were American mink and muskrat.

Table 11. The average abundance index and frequency of occurrence of semi-aquatic mammals in rivers in Lithuania.

Species	Abundance index, sings per kilometer			Frequency of occurrence, %
	Average	Maximum	Minimum	
<i>Castor fiber</i>	11.6 ± 8.92	51	2	100
<i>Lutra lutra</i>	2.4 ± 2.83	31	0	66
<i>Arvicola terrestris</i>	2.7 ± 4.90	23	0	50
<i>Neovison vison</i>	1.2 ± 3.42	9	0	25
<i>Ondatra zibethicus</i>	0.5 ± 1.95	15	0	19

The intensity of Eurasian beaver activity (abundance index) may influence the presence of American mink and muskrat (Table 12). The abundance index of Eurasian beaver was significantly higher in those river segments where these two semi-aquatic mammals were present in comparison with those segments where they were absent (for American mink: *t* test: $p = 0.046$ and muskrat: *t* test: $p = 0.01$).

Table 12. The effect of abundance index (AI) of the Eurasian beaver on the presence or absence of semi-aquatic mammal species

	<i>Lutra lutra</i>		<i>Neovison vison</i>		<i>Ondatra zibethicus</i>		<i>Arvicola terrestris</i>	
	Present	Absent	Present	Absent	Present	Absent	Present	Absent
n, river segments	46	23	17	52	13	56	35	34
Average AI of the beaver	16	12.55	20.33	13.43	20.15	12.76	15.17	14.21
Standard deviation	9.77	8.77	10.56	8.87	12.36	7.55	8.57	10.27
<i>t</i> test, <i>p</i>	0.21		0.046		0.01		0.71	

However, there was no significant association between the abundance indices of Eurasian beaver and other semi-aquatic mammals in rivers (Table 13).

Table 13. Relationship between the abundance index of the Eurasian beaver and the abundance index of semi-aquatic mammals (Pearson correlation coefficient, p -value)

Pearson correlation	<i>Lutra lutra</i>	<i>Neovison vison</i>	<i>Ondatra zibethicus</i>	<i>Arvicola terrestris</i>
r	0.09	0.11	0.19	0.09
p	0.52	0.43	0.19	0.52

3.3. Significance of beaver-made structures (lodges and burrows) for carnivores, semi-aquatic and small mammals

3.3.1. Significance of Eurasian beaver burrows to mammals of different ecological groups

Nineteen species (or taxa) of mammals were registered by camera traps as the animals were visiting beaver burrows. The bank vole was the most photographed among all the recorded mammals and the American mink was the most commonly recorded carnivore (Fig. 17, Table 14).

It took approximately 40 days from the day a camera was installed to register majority of mammal species (Fig. 17). The cumulative number of registered species increased quickly in the first 10 to 15 days, but later slowed down considerably with only a few species added thereafter.

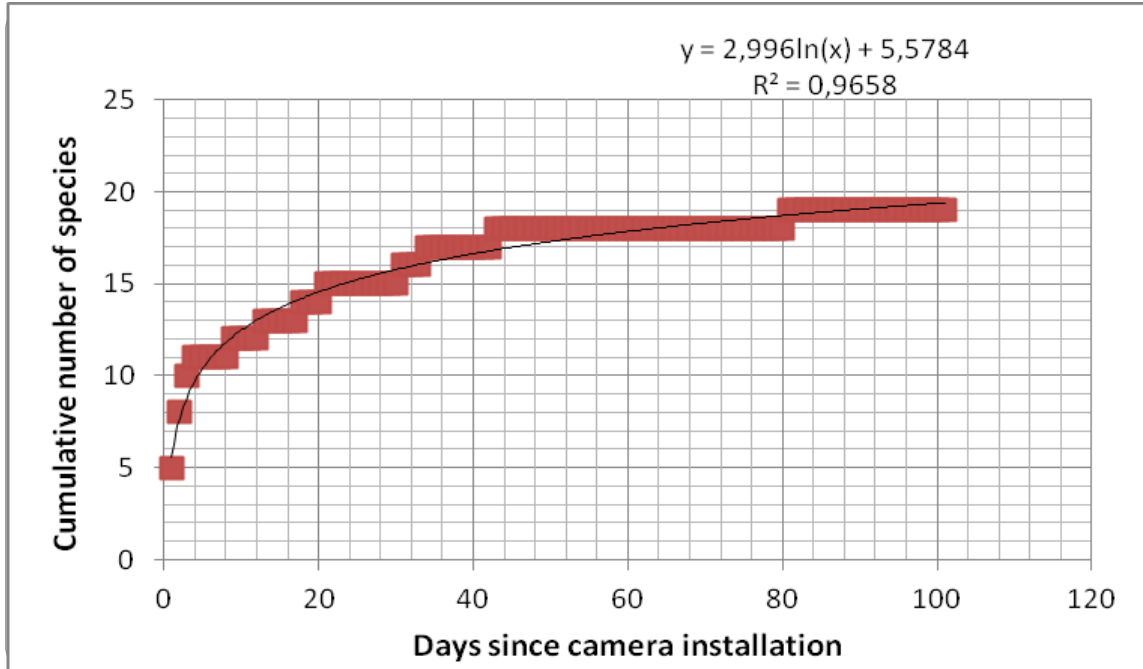


Figure 17. Cumulative number of mammal species recorded in beaver burrows versus days since camera trap installation.

First captures differed among species. Generally, rodents were the first taxa captured by cameras (Table 14). Bank voles were recorded earliest from the time of camera installation with an average of 7.8 days from the installation date. Carnivores appeared much later. For example, martens and American mink appeared on day 26.5 and 27.7, respectively.

Table 14. First photographs captured by trail cameras among mammal species since camera installation (habitats and seasons pooled together, n=37).

Species (taxa)	First trigger (mean number of days since camera installation)	Number of catching events
Small mammals		
<i>Clethrionomys glareolus</i>	7.8	37
<i>Arvicola terrestris</i>	16	5
<i>Apodemus flavicollis</i>	18	27
<i>Soricidae</i>	18.2	31
<i>Apodemus agrarius</i>	22.7	6
Carnivores		
<i>Martes spp.</i>	26.5	11
<i>Neovison vison</i>	27.7	30
<i>Lutra lutra</i>	31.6	10
<i>Mustela putorius</i>	39.6	11
<i>Nyctereutes procyonoides</i>	48.3	4
<i>Mustela spp.</i>	53.1	10
<i>Vulpes vulpes</i>	60.3	3
<i>Meles meles</i>	89	2
Others		
<i>Ondatra zibethicus</i>	13	2
<i>Sciurus vulgaris</i>	17	1
<i>Castor fiber</i>	21	1
<i>Talpa europaea</i>	51.7	3

Visitation of beaver burrows varied considerably among mammal species (Table 15). The bank vole was recorded in all camera trap events with the largest mean number of effective triggers (approximately 42 effective triggers per 30 days). No other species (taxa) demonstrated such a high frequency of occurrence and visit intensity. Three shrew species – water shrew (*Neomys fodiens*), pygmy shrew (*Sorex minutus*) and common shrew (*Sorex araneus*) – were the next most frequent group documented to visit beaver burrows. However, it was not always possible to determine which species of shrew was in a photographs, so, we have grouped all three together in the *Soricidae* group. The yellow-necked mouse had the third highest visit intensity and was second (shared with *Soricidae*) in frequency of occurrence. Small mammals obviously prevailed over carnivores in beaver burrows in term of visit intensity (Mann-Whitney: $p < 0.0001$).

Carnivores were the other major ecological group of mammals observed visiting beaver burrows (Table 15). American mink dominated among predators,

though its mean number of effective triggers was much lower than that of small mammals. However, frequency of occurrence of American mink was relatively high (73%). Martens (not distinguished between two species – stone and pine martens) as well as otter and polecat were common visitors of beaver burrows. The raccoon dog were less common at beaver burrows than mustelids.

Table 15. Visit intensity (number of effective triggers per 30 days) and frequency of occurrence (% of all taxa) of mammals in beaver burrows (habitats and seasons pooled together, $n=37$).

Species (taxa)	Mean number of effective triggers/30 days		Frequency of occurrence, %	
Small mammals				
<i>Clethrionomys glareolus</i>	41.73	Kruskal-Wallis: $p < 0.0001$	100	χ^2 : $df = 5$ $p < 0.0001$
<i>Soricidae</i>	15.20		84	
<i>Apodemus flavicollis</i>	4.66		84	
<i>Apodemus agrarius</i>	2.09		14	
<i>Microtus</i> spp.	0.14		5	
<i>Arvicola terrestris</i>	0.01		3	
Carnivores				
<i>Neovison vison</i>	1.70	Kruskal-Wallis: $p < 0.0001$	73	χ^2 : $df = 7$ $p < 0.0001$
<i>Martes</i> spp.	0.64		32	
<i>Lutra lutra</i>	0.39		30	
<i>Mustela putorius</i>	0.29		24	
<i>Nyctereutes procyonoides</i>	0.18		14	
<i>Mustela</i> spp.	0.07		11	
<i>Meles meles</i>	0.04		8	
<i>Vulpes vulpes</i>	0.04		5	
Others				
<i>Ondatra zibethicus</i>	0.01		3	
<i>Castor fiber</i>	0.01		3	
<i>Sciurus vulgaris</i>	0.01		3	
<i>Talpa europaea</i>	0.01		3	
For ecological groups:				
Small mammals	63.93	Mann-Whitney: $p < 0.0001$	100	χ^2 : $df = 1$ $p = 0.01$
Carnivores	3.35		84	

No habitat effect on visit intensity of beaver burrows was found among species or among ecological groups of mammals (Table 16). Though the mean number of effective triggers per 30 days was higher in beaver burrows in river and in wetland habitats than in beaver burrows in drainage ditches, no statistically

significant differences were observed (Kruskal-Wallis, *post hoc* analysis). The bank vole was the dominant species in all beaver burrows in all habitat types. The mean number of effective triggers per 30 days for the bank vole was higher in beaver burrows in rivers (54.02 effective triggers per 30 days) and in wetlands (50.03 triggers per 30 days) than in drainage ditches (25.53 effective triggers per 30 days), but the differences were not statistically significant (Kruskal-Wallis: $p = 0.26$). Even the *post hoc* analysis failed to show significant differences in number of effective triggers in two sample comparison.

Both seasons were pooled together in this analysis, which contributed to the variation. This decision was made to preserve larger sample sizes among habitats. However, in the future, seasons should be analyzed separately due to the strong effect of this factor on visitation.

Table 16. Visit intensity (number of effective triggers per 30 days) of mammals in beaver burrows in different habitats (seasons pooled together).

Species (taxa)*	Mean number of effective triggers per 30 days			
	Rivers n=9	Drainage ditches n=14	Wetlands n=14	Kruskal-Wallis, p
Small mammals				
<i>Clethrionomys glareolus</i>	54.02	25.53	50.03	0.2644
<i>Soricidae</i>	3.39	16.15	21.84	0.1029
<i>Apodemus flavicollis</i>	1.78	5.90	5.27	0.1229
<i>Apodemus agrarius</i>	0	5.48	0.03	0.4245
<i>Microtus</i> spp.	0	0.06	0.31	0.9504
Carnivores				
<i>Neovison vison</i>	1.20	2.90	0.83	0.7448
<i>Mustela putorius</i>	0.58	0.33	0.07	0.6101
<i>Lutra lutra</i>	0.40	0.52	0.26	0.2984
<i>Nyctereutes procyonoides</i>	0.30	0.03	0.26	0.8004
<i>Martes</i> spp.	0.10	1.34	0.27	0.5005
For ecological groups:				
Small mammals	59.18	53.13	77.48	0.3697
Carnivores	2.28	5.09	1.42	0.3879

* Only species (taxa) with mean number of effective triggers higher than 0.1 are included

Season effect was more pronounced than that of habitats, with a significant tendency of increased trigger intensity during the cold season (Table 17). Shrews showed the biggest difference between seasons (Mann-Whitney: $p = 0.009$), perhaps because in the cold season they require milder microclimate conditions (due their high-energy expenditures) and the higher availability of winter food in underground cavities. The same trend was observed for all small rodents, except the yellow-necked mouse, whose activity decreased in beaver burrows in the cold season (3.06 effective triggers per 30 days) in comparison to the warm season (6.67 effective triggers per 30 days). However, the seasonal difference for this species was not statistically significant.

Similar to the observed seasonal use of beaver burrows by small mammals, the activity of carnivores increased in the cold season (warm season = 1.39 effective triggers per 30 days; cold season = 4.26 effective triggers per 30 days). The increase was observed for all carnivores except for the raccoon dog, which hibernates during the cold season. However, the increase in number of effective triggers per 30 days was not statistically significant for carnivores (Mann-Whitney: $p = 0.21$).

Table 17. Visit intensity (number of effective triggers per 30 days) of mammals in beaver burrows in different seasons (habitats pooled together).

Species (taxa)*	Mean number of effective triggers per 30 days		
	Cold season n=21	Warm season n=16	Mann-Whitney, <i>p</i>
Small mammal			
<i>Clethrionomys glareolus</i>	53.35	26.48	0.1010
<i>Soricidae</i>	24.20	3.38	0.0092
<i>Apodemus agrarius</i>	3.53	0.19	0.7130
<i>Apodemus flavicollis</i>	3.06	6.76	0.1109
Carnivore			
<i>Neovison vison</i>	2.33	0.88	0.9511
<i>Martes</i> spp.	0.95	0.22	0.6347
<i>Lutra lutra</i>	0.56	0.17	0.4254
<i>Mustela putorius</i>	0.42	0.12	0.1253
<i>Microtus</i> spp.	0.21	0.06	0.9633
<i>Nyctereutes procyonoides</i>	0.18	0.19	0.6902
For ecological groups:			
Small mammals	84.35	36.86	0.0073
Carnivores	4.26	1.39	0.2144

* Only species (taxa) with mean number of effective triggers higher than 0.1 are included.

3.3.2. The 24-hour activity of the most abundant mammals in beaver burrows

Bank vole was active in beaver burrows all day in both seasons (Fig. 18). The 24-hour activity of the bank vole was significantly greater in cold season than in warm (Wilcoxon: $p < 0.001$). By analyzing differences between period of darkness and light, we have found statistically significant differences of 24-hour activity of bank vole between the warm and the cold seasons (χ^2 test: $df = 1$, $p = 0.002$). It looks like that in warm season, bank vole spends relatively more time in the burrow, while in cold season, the activity per hour seems to be similar both at night and at day. In warm season, three activity peaks of the bank vole can be distinguished – before the sunrise, after the sunrise and after the sunset. Same three activity peaks of bank vole could be distinguished in cold season too - before the sunrise, after the sunrise and after the sunset, but the 24-hour activity shifts in time, because of the later sunrise and earlier sunset.

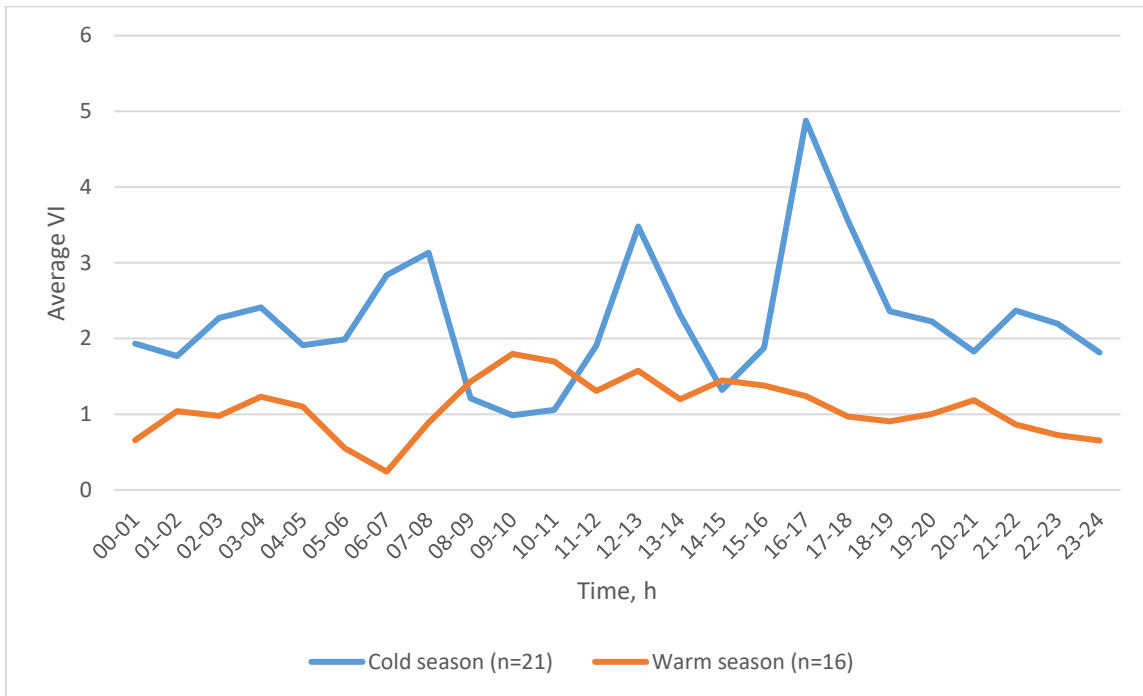


Figure 18. The 24-hour activity (average visiting intensity (VI) per hour) of bank vole in beaver burrows in cold and warm seasons.

Shrews were active in beaver burrows all day in both seasons (Fig. 19) but the 24-hour activity was greater in winter than in summer (Wilcoxon: $p < 0.001$). By analyzing differences between period of darkness and light, no activity peaks of shrews may be distinguished in warm, meanwhile in cold season, shrews were more active at night than at day, but there was no statistically significant differences of 24-hour activity of bank vole between the warm and the cold seasons (Fisher's χ^2 test: $df = 1, p = 0.28$).

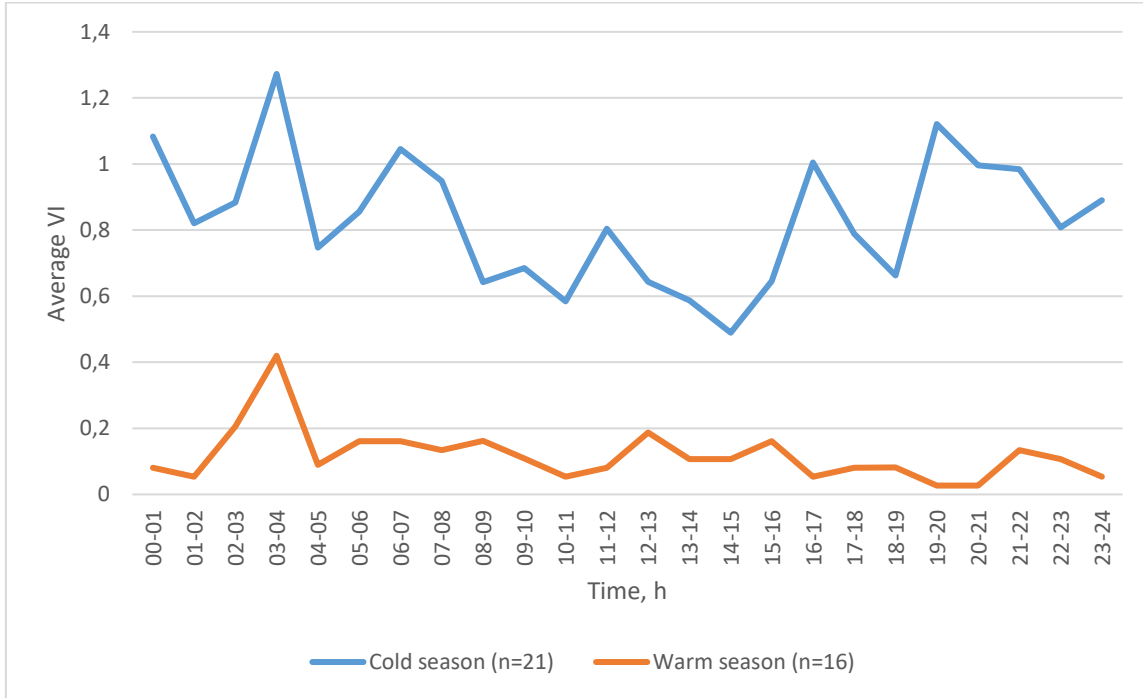


Figure 19. The 24-hour activity (average visiting intensity (VI) per hour) of *Soricidae* in beaver burrows in cold and warm seasons.

The yellow-necked mouse was more active in beaver burrows in warm season than in cold (Wilcoxon: $p = 0.005$). Both in warm and in cold seasons, this species was active after the sunset only (Fig. 20). Although the yellow-necked mouse was active in beaver burrows from the sunset to sunrise in warm season, while in cold season, from the sunset to the midnight, the patterns of diurnal activity did not differ significantly (Fisher's χ^2 test: $df = 2, p = 1$).

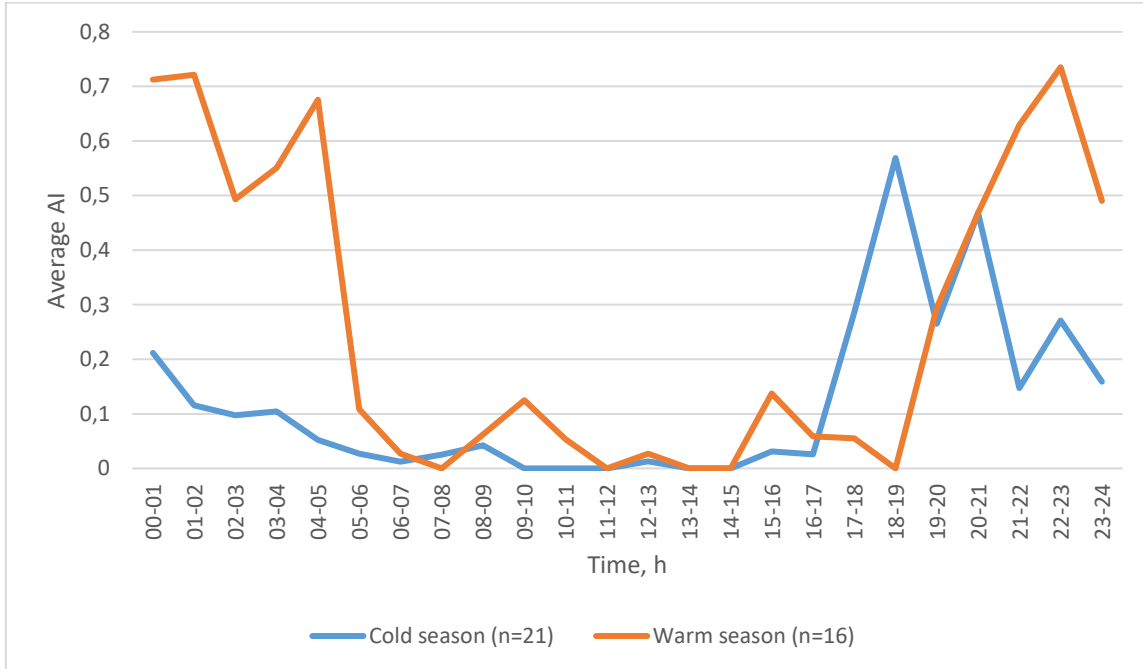


Figure 20. The 24-hour activity (average visiting intensity (VI) per hour) of yellow-necked mouse in beaver burrows in cold and warm seasons.

American mink was active in beaver burrows all day both in warm and in cold seasons, but it was more active in cold season than in warm (Wilcoxon: $p < 0.001$) (Fig. 21). In cold season, the activity at night and at day did not differ significantly from warm season.

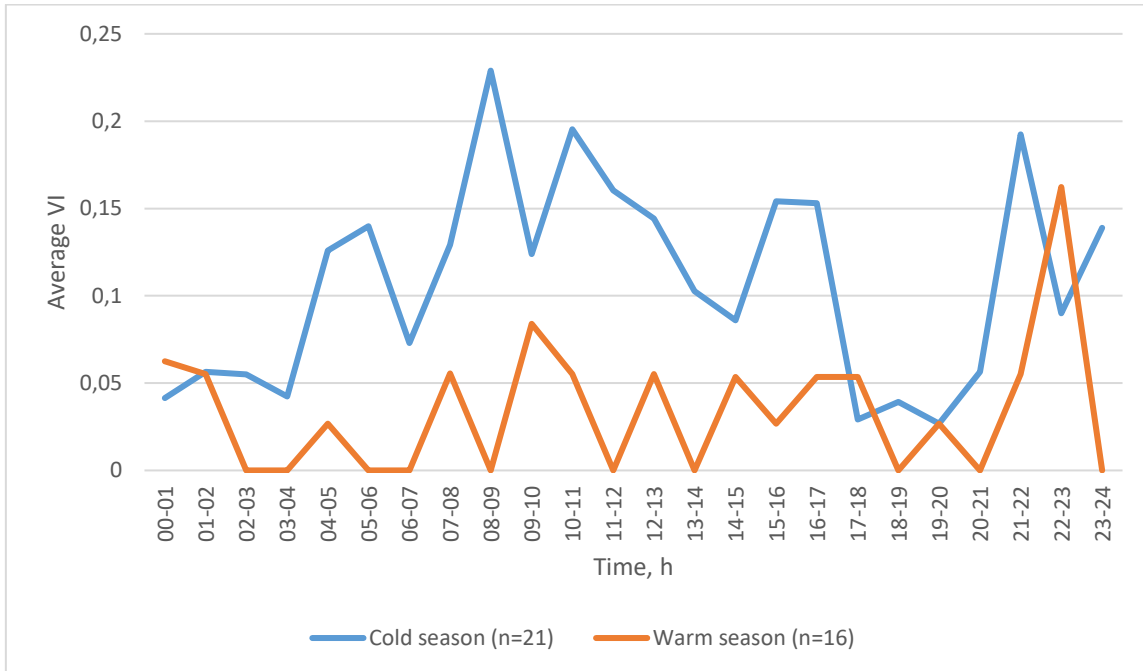


Figure 21. The 24-hour activity of American mink (average visiting intensity (VI) per hour) in beaver burrows in cold and warm seasons.

3.4. Mammals on beaver lodges

3.4.1. American mink on beaver lodges

Occurrence of American mink on beaver lodges in peripheral beaver sites varied among the years (Table 18). For example, American mink were rarely documented on beaver lodges in 2011, but their presence increased to 75% of all studied lodges by 2013. These findings demonstrate two things: 1) attractiveness of beaver lodges as shelter or a feeding place for American mink; 2) some other factors can influence presence of this invader in peripheral habitats.

Table 18. Frequency of occurrence (%) of American mink on beaver lodges in peripheral beaver sites in the Molétai study area in 2009 to 2014.

Indicator	Year						χ^2 test
	2009	2010	2011	2012	2013	2014	
Total number of studied beaver site	35	34	37	no data	40	25	$\chi^2 = 46.449$ $df = 4$ $p < 0.0001$
Total number of beaver site with the signs of American mink	12	14	1		30	8	
Frequency of occurrence	34,3	41,2	2,7		75,0	32,0	

3.4.2. Small mammals on beaver lodges

A total of eleven species of small mammals were caught on beaver lodges and five species in the forest during the research period (Table 19). The greatest trapping success in both habitats was recorded for the bank vole (*Clethrionomys glareolus*), followed by the common shrew (*Sorex araneus*) and the yellow-necked mouse (*Apodemus flavicollis*) on beaver lodges. In the forest, these two subdominant species were interchanged: the trapping success for the yellow-necked mouse was higher than for the common shrew. These three species also had the highest frequencies of occurrence in both habitats.

The short-tailed vole (*Microtus agrestis*) was relatively common on beaver lodges, but rarely caught in the forest. The remaining species had lower trapping success and occurrence on beaver lodges and were never caught in the forest (except the rarely detected harvest mouse (*Micromys minutus*)). For all species and in both habitats the trapping success was variable and the standard deviation was higher than the mean, indicating that a number of factors were involved.

Seasonal analysis of the trapping success of small mammals resulted in variability of this parameter considerably, especially for species with higher trapping success rates (Table 19). Seasonally, the most expressed differences in trapping success between beaver lodges and forest habitat were found for the common shrew. In three seasons – summer, autumn and winter – the trapping success of common shrews was significantly higher on beaver lodges than in the

forest, especially in winter (Table 19). The bank vole showed highest overall trapping success, but differences in trapping success of this species between habitats were not as obvious in any season. Despite the slightly higher trapping success for bank voles on beaver lodges than in the forest during all seasons, statistically significant differences were found only in autumn. The yellow-necked mouse recorded the third highest trapping success rates; however, it showed opposite tendencies between habitats. During all seasons, it was slightly more abundant in the forest than on beaver lodges. In autumn this difference was close to the confidence level (Mann-Whitney test, $p = 0.07$).

The total trapping success for the small mammal community on beaver lodges was higher than in the forest in all seasons, but statistically significant differences were observed only in autumn (Mann-Whitney: $p = 0.001$). Species diversity of small mammals was higher on beaver lodges than in the forest in all seasons, but no significant differences were observed (Table 19).

Table 19. An average trapping success (individuals per 100 traps per night) (mean TS±SD) and diversity of small mammal (Shannon’s diversity index H') on beaver lodges and in the forest in different seasons in 2007-2011. Statistically significant differences – in bold (Mann-Whitney test).

Species	Beaver lodges TS±SD vs Forest TS±SD							
	Spring		Summer		Autumn		Winter	
	n=44	n=39	n=47	n=39	n=47	n=39	n=42	n=33
<i>Clethrionomys glareolus</i>	5.76±3.41	4.27±2.52	13.48±5.19	11.97±3.89	22.55±5.31	10.77±3.04	5.71±1,39	2.42±7.48
	p=0.95		p=0.94		p<0.0001		p=0.99	
<i>Sorex araneus</i>	0.76±0.86	0	2.84±1.95	0.17±0.36	2.55±1.20	0.85±0.73	5.71±1.54	0.61±2.77
			p=0.002		p=0.005		p=0.001	
<i>Apodemus flavicollis</i>	0.45±0.74	1.03±1.01	1.84±1.34	2.39±1.30	2.41±1.93	5.64±2.30	0	0.81±9.13
	p=0.30		p=0.40		p=0.02		p=0.001	
<i>Microtus agrestis</i>	0.3±0.67	0.17±36	2,13±2.23	0	0.99±0.92	0	0.16±0.15	0
<i>Apodemus agrarius</i>	0.15±0.33	0	0.15±0.32	0	0.99±1.13	0	0	0
<i>Neomys fodiens</i>	0	0	0.28±0.45	0	0.43±0.72	0	0.16±0.15	0
<i>Mus musculus</i>	0	0	0.14±0.32	0	0	0	0	0
<i>Microtus arvalis</i>	0	0	0.14±0.32	0	0.14±0.32	0	0	0
<i>Microtus oeconomus</i>	0	0	0.28±0.45	0	0.43±0.72	0	0.16±0.15	0
<i>Sorex minutus</i>	0	0	0	0	0.28±0.45	0.17±0.36	0	0
<i>Micromys minutus</i>	0	0	0	0	0.14±0.32	0	0	0
TS of sm. mammal community:	7.42±3.50	5.47±2.92	21.28±6.29	15.89±4.29	30.92±6.48	17.44±3.77	11.09±4.73	3.48±2.42
	p=0.89		p=0.25		p=0.001		p=0.29	
H'	0.809	0.616	1.213	0.511	1.066	0.855	0.879	0.81

The small mammal community was different on beaver lodges from that in the forest habitats (Fig. 22). The most pronounced differences were found in summer (χ^2 - test: df = 4, p < 0.001), autumn (χ^2 test: df = 4, p = 0.001) and in winter (χ^2 test: df = 4, p =0.004). Bank voles were captured more often in both habitat types during all seasons except on beaver lodges in winter. The yellow-necked mouse was caught more often in the forest habitats than on beaver lodges, while the common shrew was caught more often on beaver lodges than in forest habitats. Other small mammal species comprised less than 15% of captures in both habitat types. One more peculiarity of community structure in the forest was

that the share of other species was nearly zero, whereas on beaver lodges other species taken together have contributed significantly to the species composition, especially in summer and autumn.

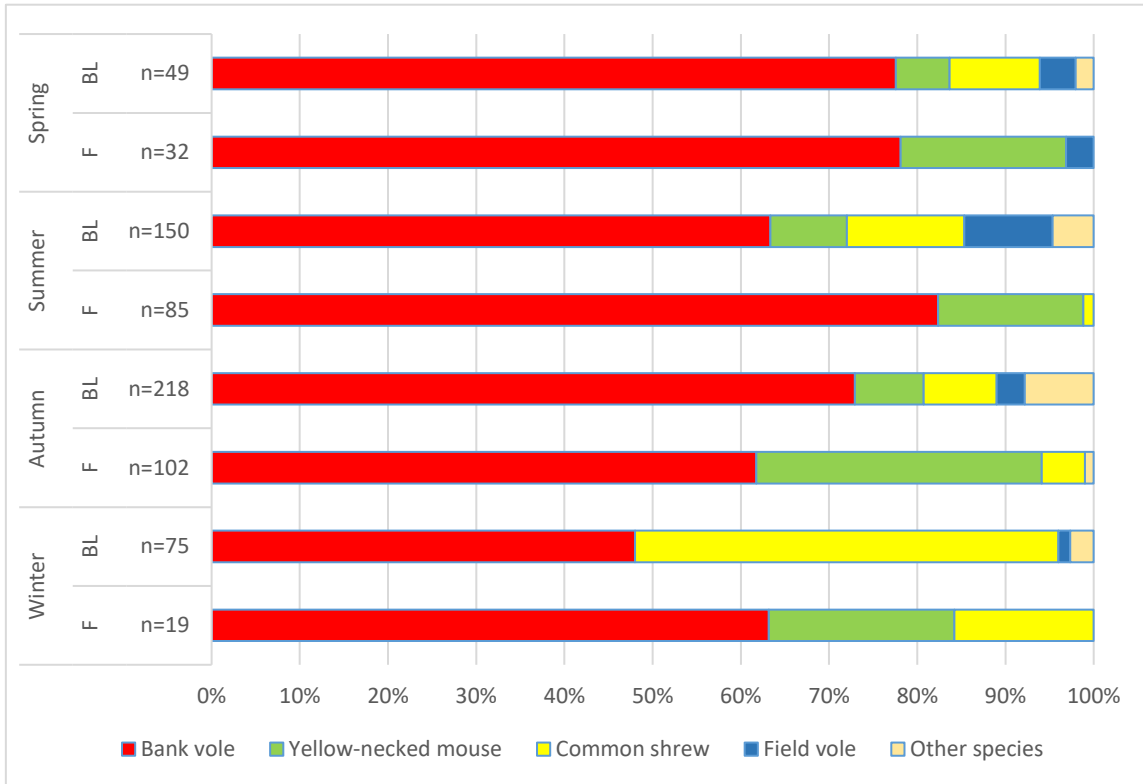


Figure 22. The structure of small mammal communities on beaver lodges (BL) and in the forest (F) in different seasons.

Seasonal variations in small mammal community structure were more pronounced on the beaver lodges (Yates' χ^2 test: $df = 12$, $p < 0.001$) than in the forest (Yates' χ^2 test: $df = 12$, $p < 0.07$). On the beaver lodges, the core of the community was formed predominantly by three species (bank vole, common shrew and yellow-necked mouse). The contribution to the total small mammal community of other species was also more significant on beaver lodges than in the forest. In the forest, the dominant bank vole and subdominant yellow-necked mouse formed the core of the small mammal community.

3.5. Demographic and helminthological status parameters of small mammals in beaver-modified habitats

3.5.1. Demographic parameters of bank vole caught on beaver lodges

The age structure of bank voles trapped on beaver lodges was similar to that in the forest in all seasons except winter (χ^2 test: $df = 2$, $p = 0.048$) (Fig. 23). In winter, no juveniles were caught on beaver lodges while in the forest more than 20% of bank voles captured were assigned to this age group.

The seasonal changes of bank vole age structure were strongly expressed both on beaver lodges (χ^2 test: $df = 6$, $p < 0.001$) and in the forest (χ^2 test: $df = 6$, $p < 0.001$). The proportion of adult bank voles decreased significantly from spring to autumn and stabilized in winter in both habitats, while the proportion of immature individuals was increasing in the same period. In winter, the decrease in the proportion of juveniles captured on beaver lodges was significant (χ^2 test: $df = 2$, $p < 0.001$). The changes in age structure were not significant in the forest between the autumn and winter seasons.

The proportion of both male and female in the populations of bank vole did not differ between different habitats and different seasons. The ratio of male to female in both habitats was 1:1 and remained stable whole year (Fig. 24).

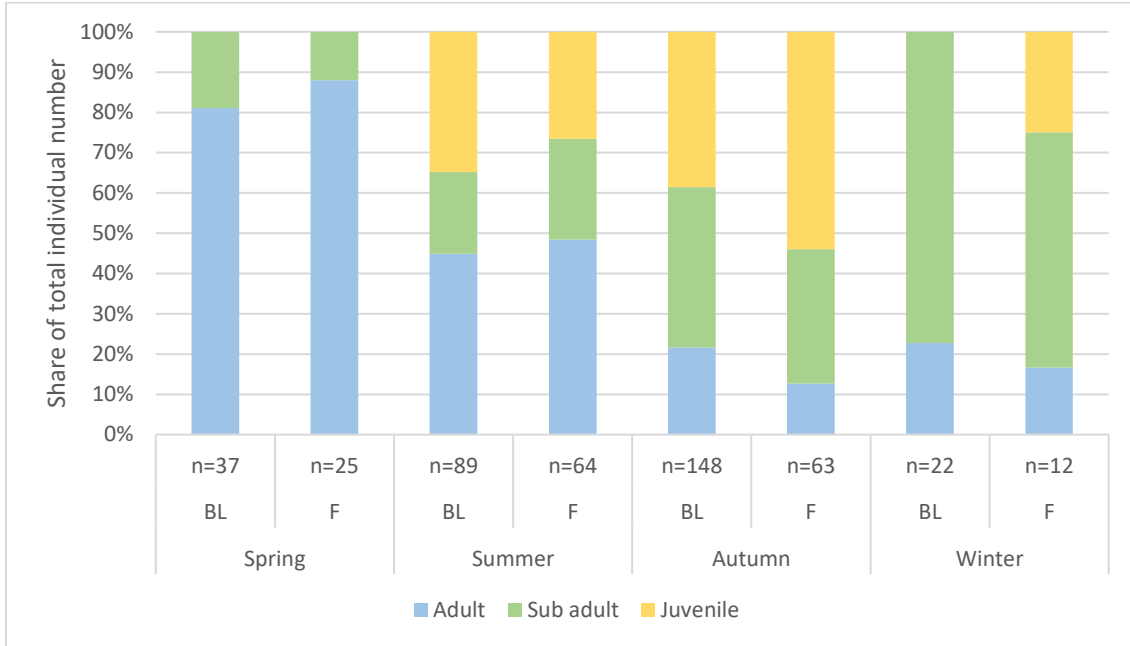


Figure 23. Seasonal dynamics of age structure of all bank voles trapped on beaver lodges (BL) and in the forest (F) during different seasons.

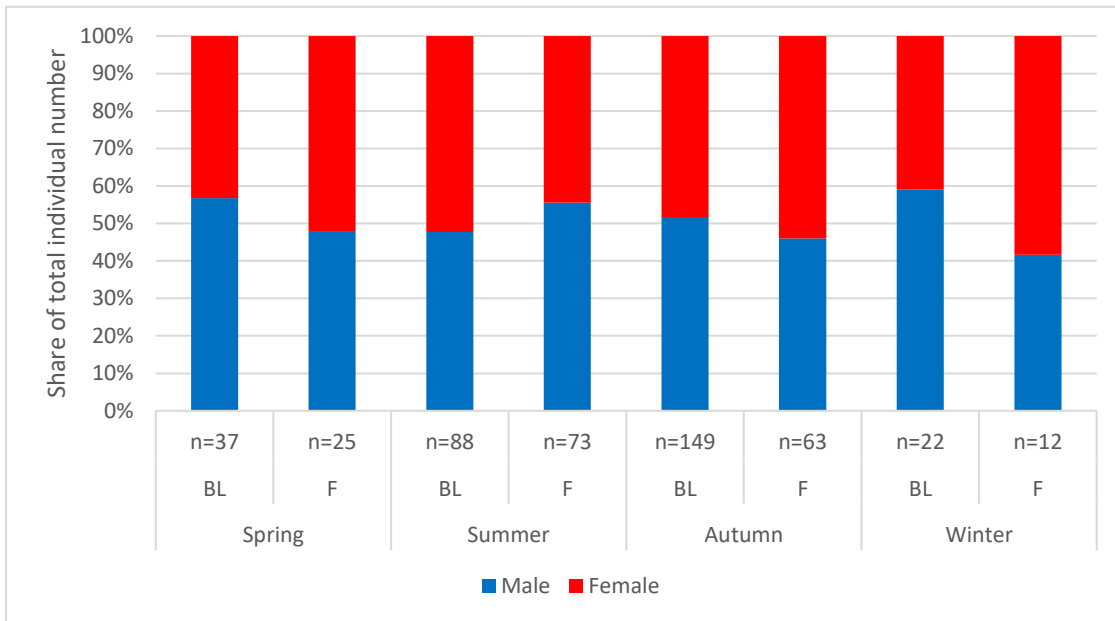


Figure 24. Seasonal dynamics of sex ratio of all bank voles on beaver lodges (BL) and in the forest (F) in different seasons.

For adult bank voles the sex ratio also did not differ between habitats during seasons (Fig. 25). However we did observe significant seasonal changes in the sex ratio of adult bank voles on beaver lodges (χ^2 test: $df = 3, p = 0.05$), but did not observe these fluctuations in the forest (χ^2 test: $df = 3, p = 0.13$). Both on beaver lodges and in the forest, no adult female bank voles were caught in winter.

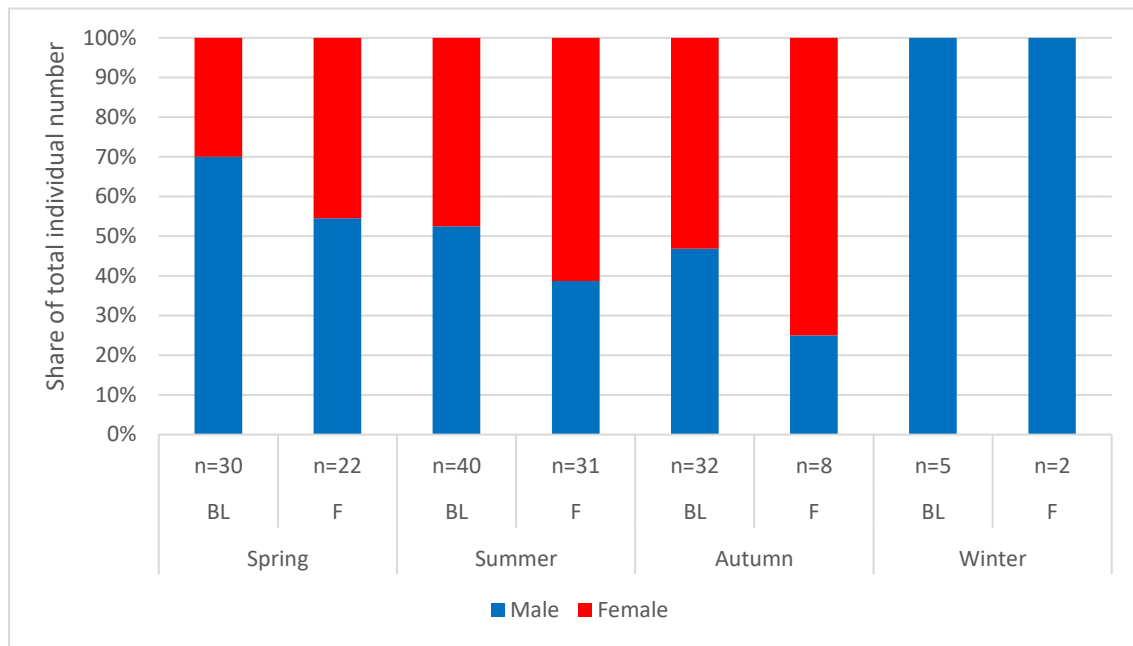


Figure 25. Seasonal dynamics of sex ratio of adult bank voles on beaver lodges (BL) and in the forest (F) in different seasons.

3.5.2. Helminthological status of bank vole and yellow-necked mouse populations on beaver lodges

For both small rodent species (bank vole and yellow-necked mouse) and for both treatments (beaver sites and forest), 66 % of the individuals of small rodent were infected by helminths. Helminths of 10 species and 3 other taxa (5821 specimens) were found: 1 cestode (tapeworms), 6 nematodes (hookworm), 2 trematodes (fluke) species and 1 cestode and 2 nematodes of other taxa (Table 20).

Bank voles were infected by 8 species (or other taxa) of helminths and there was no difference in the number of helminth species between bank voles caught at beaver sites and in the forest. All parasite species were the same in both habitats for the bank vole (Table 20).

Yellow-necked mice were infected by 7 helminth species (or other taxa) at beaver sites and six – in the forest. The nematode *Syphacia montana* was found only in mice at beaver sites (Table 20).

Table 20. Helminth species (or other taxa) composition and their distribution among hosts from beaver sites and the forest

Class	Family	Helminth species or other taxa	Beaver sites		Forest	
			<i>Clethrionomys glareolus</i>	<i>Apodemus flavicollis</i>	<i>Clethrionomys glareolus</i>	<i>Apodemus flavicollis</i>
Cestoda	Taeniidae	<i>Hydatigera taeniaeformis</i>	+	-	+	-
		<i>Cestoda g. sp.</i>	+	+	+	+
Nematoda	Capillariidae	<i>Capillaria sp.</i>	+	-	+	-
	Heligmosomatidae	<i>Heligmosomum costellatum</i>	+	+	+	+
		<i>Heligmosomum mixtum</i>	+	+	+	+
	Syphaciidae	<i>Syphacia montana</i>	-	+	-	-
		<i>Syphacia petruszewiczi</i>	+	-	+	-
		<i>Syphacia stroma</i>	-	+	-	+
		<i>Syphacia sp.</i>	-	+	-	+
Trichocephalidae	<i>Trichocephalus muris</i>	+	-	+	-	
Trematoda	Plagiorchidae	<i>Plagiorchis elegans</i>	-	+	-	+
	Notocotylidae	<i>Notocotylus noyeri</i>	+	-	+	-
Total number of helminth species			8	7	8	6

Analyzing the presence of specific helminth species in different seasons, the mean abundance index showed only slight and statistically insignificant differences between habitats (Table 21), except for two cases where bank voles were more heavily infected by *Syphacia petrusewiczii* at beaver sites than in the forest (Mann-Whitney test: autumn, $p = 0.03$ and winter, $p = 0.02$). In all other cases, the mean abundance of helminths in bank voles in different habitats was similar (Table 21).

Total mean abundance of all parasites in the bank vole indicated a higher infection level at beaver sites than in the forest, especially in winter (Mann-Whitney test: winter, $p = 0.049$). A similar tendency was observed in the yellow-necked mouse, which had a higher abundance of all parasites in autumn. However, these differences between habitats were not statistically significant (Table 21).

Table 21. Mean abundance of helminths in small rodents at beaver sites and in the forest in different seasons (n – number of dissected individuals of small rodents, B – beaver sites, F – forest)

Helminth species or other taxa	Habitat	<i>Clethrionomys glareolus</i>				<i>Apodemus flavicollis</i>			
		Spring n=23(B) n=22(F)	Summer n=26(B) n=43(F)	Autumn n=66(B) n=80(F)	Winter n=13(B) n=14(F)	Spring n=3(B) n=12(F)	Summer n=8(B) n=18(F)	Autumn n=10(B) n=46(F)	Winter n=0(B) n=6(F)
<i>Capillaria</i> sp.	B	-	-	0.3	-	-	-	-	-
	F	-	-	0.3	-	-	-	-	-
<i>Cestoda</i> g. sp.	B	0.09	0.07	0.1	0.2	0.3	-	0.2	-
	F	0.1	0.2	0.09	0.07	0.3	0.06	0.1	-
<i>Heligmosomum mixtum</i>	B	6.3	0.5	1.2	4.2	1.3	0.3	1.0	-
	F	4.6	1.4	2.8	2.4	3.0	0.7	0.4	4.7
<i>Heligmosomum costellatum</i>	B	-	1.0	1.1	-	-	0.3	-	-
	F	-	2.6	0.8	-	-	0.2	0.4	-
<i>Hydatigera taeniaeformis</i>	B	0.09	-	-	-	-	-	-	-
	F	0.05	-	-	-	-	-	-	-
<i>Notocotylus noyeri</i>	B	13.4	0.7	0.08	-	-	-	-	-
	F	11.0	0.09	0.01	-	-	-	-	-
<i>Plagiorchis elegans</i>	B	-	-	-	-	-	0.4	-	-
	F	-	-	-	-	-	0.2	0.04	-
<i>Syphacia montana</i>	B	-	-	-	-	-	12.3	2.0	-
	F	-	-	-	-	-	-	-	-
<i>Syphacia petrusewiczii</i>	B	6.1	18.6	8.9*	9.8*	-	-	-	-
	F	-	14.2	2.4*	0.1*	-	-	-	-
<i>Syphacia stroma</i>	B	-	-	-	-	-	3.8	1.0	-
	F	-	-	-	-	2.8	11.8	3.6	7.7
<i>Syphacia</i> sp.	B	-	-	-	-	10.7	-	-	-
	F	-	-	-	-	0.3	0.7	4.0	0.5
<i>Trichocephalus muris</i>	B	0.04	-	0.02	0.08	-	-	-	-
	F	-	-	0.01	0.07	-	-	-	-
Totally for all helminth species	B	26.0	20.5	12.2	14.2*	1.7	16.9	22.5	-
	F	15.8	18.5	6.6	2.7*	6.4	13.6	8.5	12.8

* – statistically significant

Similarly, the prevalence of infection did not revealed any significant differences between habitats during different seasons in all cases, except two (Table 22). Controversial index of infection prevalence was found in bank voles infected by *Syphacia petrusewiczii* and *Heligmosomum mixtum*. The index for *Syphacia petrusewiczii* in bank voles in autumn was significantly higher at beaver sites (χ^2 test: $df = 1$, $p = 0.0023$), but for the *Heligmosomum mixtum* in the same host and in the same season it was higher in the forest (χ^2 test: $df = 1$, $p = 0.0108$). For the remainder of the differences in parasite species infection prevalence

between two habitats in different seasons was not significant for either rodent species.

Table 22. Infection prevalence (%) of helminths in small rodents at beaver sites (B) and in the forest (F) in different seasons (n – number of dissected individuals of small rodents)

Helminth species or other taxa	Habitat	<i>Clethrionomys glareolus</i>				<i>Apodemus flavicollis</i>			
		Spring n=23(B) n=22(F)	Summer n=26(B) n=43(F)	Autumn n=66(B) n=80(F)	Winter n=13(B) n=14(F)	Spring n=3(B) n=12(F)	Summer n=8(B) n=18(F)	Autumn n=10(B) n=46(F)	Winter n=0(B) n=6(F)
<i>Capillaria</i> sp.	B	-	-	4.5	-	-	-	-	-
	F	-	-	5.0	-	-	-	-	-
<i>Cestoda</i> g. sp.	B	8.7	8.3	3.0	23.1	33.3	-	10.1	-
	F	9.1	20.9	8.8	7.1	33.3	5.6	6.5	-
<i>Heligmosomum mixtum</i>	B	43.5	19.2	21.1*	77.0	66.7	12.5	30.0	-
	F	68.2	32.6	42.5*	57.1	25.0	11.1	13.0	33.3
<i>Heligmosomum costellatum</i>	B	-	7.7	9.1	-	-	12.5	-	-
	F	-	20.9	10.0	-	-	5.6	6.5	-
<i>Hydatigera taeniaeformis</i>	B	4.5	-	-	-	-	-	-	-
	F	4.5	-	-	-	-	-	-	-
<i>Notocotylus noyeri</i>	B	17.4	7.7	1.5	-	-	-	-	-
	F	18.2	2.3	1.3	-	-	-	-	-
<i>Plagiorchis elegans</i>	B	-	-	-	-	-	25.0	-	-
	F	-	-	-	-	-	5.6	2.2	-
<i>Syphacia montana</i>	B	-	-	-	-	-	25.0	10.1	-
	F	-	-	-	-	-	-	-	-
<i>Syphacia petruszewiczi</i>	B	13.0	30.8	25.6*	30.8	-	-	-	-
	F	-	14.0	6.3*	14.3	-	-	-	-
<i>Syphacia stroma</i>	B	-	-	-	-	-	25.0	10.1	-
	F	-	-	-	-	33.3	5.6	13.0	16.7
<i>Syphacia</i> sp.	B	-	-	-	-	33.3	-	-	-
	F	-	-	-	-	16.7	5.6	15.2	16.7
<i>Trichocephalus muris</i>	B	4.3	-	1.5	7.7	-	-	-	-
	F	-	-	1.3	7.1	-	-	-	-
Totally for all helminth species	B	73.9	61.5	60.6	76.9	100.0	75.0	50.0	-
	F	86.4	74.4	70.0	64.3	75.0	33.3	34.8	50.0

We found 3 dominant species of helminths in the bank vole and 4 species in the yellow-necked mouse. Domination pattern of helminth species in the bank vole varied more among seasons, but less between the two tested habitats, except in autumn and winter. *Syphacia petruszewiczi* was dominant in bank voles at beaver sites during summer, autumn and winter, but only during summer in the

forest habitat. These rodents had the same dominant helminth species in the two habitats during spring and summer, but not during autumn and winter.

The helminth community diversity indices for the bank vole were slightly higher at beaver sites ($H' = 1.27$; infected by 8 helminth species) than in the forest ($H' = 1.11$; also infected by 8 helminth species).

4. DISCUSSION

4.1. The impact of the Eurasian beaver on landscape and habitat structure

The density of beaver sites is higher in study area than in neighboring countries. According to Czech and Lisle (2003), the highest density of beaver sites in some parts of Poland may reach 10 sites per 1000 hectares. Beaver site densities in Sweden reported by Hartman (1994) were up to 2 sites per 1000 hectares, while 5 beaver sites per 1000 hectares were reported by Balodis (1990) in Latvia. The high density of the beaver site in our study area may be caused by the location of Lithuania relative to the range of the species, specific local ecological conditions and the carrying capacity of the landscape (Ulevičius, 2001a; Bluzma, 2003). The countries, which are on the periphery of the beaver range, could have higher densities of beaver sites due to reduced opportunities for young beavers to spread (Hartman, 1994). Whereas, Lithuania is not on the periphery of the beaver range and therefore the density of beaver sites is determined by the carrying capacity of the landscape.

The densities of beaver sites are not continuous in Lithuania. According to Ulevičius (2008), higher densities of beaver sites are more common to the hilly landscape in the western and eastern parts of Lithuania. The depressions between the hills that have high groundwater levels are a common element of the hilly landscape (Basalykas, 1977). Due to this factors, the density of the beaver sites are

higher in hilly morainic landscape than in other types of the landscape in Lithuania. In our study area (100 km²), the estimated beaver site density was similar to the highest densities reported in other parts of western and eastern parts of Lithuania (Bluzma, 2003; Ulevičius, 2008), where the density was 20 beaver sites per 1000 hectares.

Not all wetlands in our study area were inhabited by Eurasian beavers (55% of wetlands had visible activity). The factor most limiting the establishment of a beaver site could be grouped into two categories: 1) important, such as carrying capacity of the environment, anthropogenic influence, presence of permanent water body, stream gradient, speed of the water flow, etc. and 2) essential such as riparian vegetation and interaction among beavers (Kitchener, 2001; Dewas *et al.*, 2011). The interaction of these factors may influence the home range of the beavers (Fustec *et al.*, 2001) and the attractiveness of the wetland. Thus, less attractive wetlands are free of beavers in the study area.

Another factor influencing colonization and spread could be the size of the water body. According to Johnston and Naiman (1990c), who examined North American beavers in Minnesota, found, that the most preferable beaver ponds are 1 to 2 hectares in size, although beavers also were found in ponds smaller than 1 hectare. In our study area, more than 87% of wetlands that were smaller than 1 ha were vacant while 70% of wetlands greater than 1 ha were inhabited. Therefore, it could be that the attractiveness of smaller water bodies may increase when beaver population become denser. The remaining question is if the Eurasian beaver will spread to smaller wetlands or all vacant wetlands, that are smaller than 1 ha in the study area. There is no simple answer to this question, since the suitability of a wetland for beaver occupation depends on slope, soil type of the shore, and water depth (Hartman, 1996; Ulevičius *et al.*, 2009). Data on the slope of the shore and depth of the water bodies were not collected during our research, so the suitability of the wetland could not be estimated using these parameters.

The type of wetland could also be a factor determining the absence (or presence) of beavers. Reed and sedge wetlands may require more effort to establish a beaver site and to create associated infrastructure if there are no drainage ditches nearby. While in open water wetlands and in shrubby fens, the movement and activity of beavers are less limited.

The size of the beaver site depends on two factors: 1) the area of the wetland and 2) the land area affected by beaver. The area of the wetland depends mostly on the relief of the territory and could be easily estimated from the orthophotos (Johnston, Naiman, 1990a; Bluzma, 2003). Meanwhile the extent of land affected by beavers is estimated by measuring the farthest point from the shore beavers traveled to cut woody vegetation, which is influenced by the surrounding vegetation (Jenkins 1980; Allen, 1982; Fustec *et al.*, 2001, Raffel *et al.*, 2008). According to Jenkins (1980), North American beaver may travel more than 100 m from the shore to browse oak, maple, birch and witch-hazel species. Plants, that are more preferable to beaver, are grazed at a greater distance than less preferable plants. Other studies showed that the most heavily grazed trees are within 20 m from the water (Kostkan, Lehky, 1997; Hood, Bayley, 2008). Allen (1982) defines the minimum land area affected by beaver as the minimum amount of contiguous habitat and the maximum is in a range of 200 m from the shore. The distances between the grazed plants and the water bodies, found in our research, fall in the range given by other authors. In our study area, the farthest plants grazed by beavers were common aspens and willows (50 to 51 meters from the shore). Beavers traveled shorter distances from the shore to graze on less preferred species like common hazel, birches and oak. The most intense grazing activity of the beaver was observed between 10 to 20 meters from the water body, which was similar to distances reported by Kostkan and Lehky (1997) in Czech Republic and Hood and Bayley (2008) in Canada.

The damming activity of the beavers occurs in small river streams with slow water flow (Naiman *et al.*, 1986). While choosing the places for constructing

the dams, the most important factors were the physical characteristics of the stream channel (width, depth, and slope) and the drainage basin (watershed area or the area of the channel cross section) (Zavyalov, 2014). The number of dams per length of the river depends on the density of the beaver in the area and other natural and anthropogenic factors. One beaver family may build from 1 to 10 beaver dams per beaver site (Ulevičius *et al.*, 2009). According to Ulevičius *et al.* (2009), the average density of beaver dam per 10 kilometer was 2.1 in central Lithuania, in a flat landscape. The density of dams was 6 dams per 10 kilometer in the hilly morainic landscape of eastern Lithuania. In different regions of Russia, the density of beaver dams in land reclamation canals varies from 17 to 45 dams per 10 kilometers (Aleinikov, 2007). As a result of the damming activity, the area of beaver made habitats and beaver ponds, is significantly greater in highly morainic landscape than on the plains, which contributes to a greater landscape diversity.

The size of the beaver pond is determined by the geomorphological specificities of the territory (Johnston, Naiman, 1987; Zavyalov, 2014). Small-area beaver ponds are common to narrow river valleys (Zavyalov, 2014), while large-area beaver ponds are the elements of swamped floodplains (Johnston, Naiman, 1987). The drainage ditches are the equivalent to small rivers. Thus, in the study area in eastern Lithuania, the size of the beaver pond varies from 0.03 ha up to 0.69 ha in drainage ditches. Similar size of the beaver ponds (an average of 0.08 ha) were observed in land reclamation canals in Belarus (Yanuta, 2007).

Beavers can significantly affect the landscape. According to Johnston and Naiman (1990a), North American beaver can modify more than 4% of the landscape in a decade by creating new water bodies. In North America, after the appearance of the beaver in Voyageurs National Park, Minnesota, (250 hectares), the total area of water impounded by beaver increased from 1% to 13% (Johnston, Naiman, 1990a; 1990b; 1990c). In their study area, more than 60% of affected territory consists of beaver ponds and about 40% was changed or affected adjacent

terrestrial habitats. In our study, we found that wetlands occupied by Eurasian beaver compose more than 7% of the area, while the dry land from 3% to 5% of the area. The ratio of wetlands and terrestrial habitats affected by Eurasian beaver was similar to that observed for North American beaver in Minnesota. The total impact of Eurasian beaver is estimated to be more than 12% of the area in the eastern Lithuania, which is similar to the impact of North American beaver in Minnesota.

4.2. The effect of beaver on density and distribution of mammals of different ecological groups

The structure of the landscape may determine the total number of mammal species that can be found in an area as well as the abundance of some species (Bluzma, Baleišis, 1999; Andren, 2013), because the availability of food sources and shelters are closely related to landscape structure (Said, Servanty, 2005). According to the behavioral plasticity theory, the fragmentation of habitats or the variety of different habitats in a territory has positive impacts on the abundance of generalist species (Komers, 1997). Generalist herbivores and predators use open areas for feeding and woodlands for cover (Kurki *et al.*, 1998; Hewison *et al.*, 2001; Jepsen, Topping, 2004), so the abundance of animals among the habitats may remain similar. For habitat specialists, the fragmentation of the habitat has negative impacts if the distance between the habitats is greater than their dispersal range, or there are no ecological corridors between the habitats (Andren, 2013). We found similar patterns during our study. The generalists like roe deer, red fox and European hare have similar abundance indices in different habitat types, while specialists, such as elk and American mink, preferred beaver wetlands and mosaic landscapes where Eurasian beavers have modified approximately 10% of the area.

The abundance and community structure of cervids depends on various landscape characteristics (Bluzma, Baleišis, 1999). The abundance of cervids is

greater in hilly morainic landscape than on sandy plains or clay plains. According to Baleišis and Bluzma (1999), the greater abundance of roe deer is due to habitat fragmentation and the greater variety of habitats in highly morainic landscapes. Our study found that the presence of the Eurasian beaver increases the diversity of habitats at the landscape scale. This increase in diversity can explain the greater abundance of roe deer in the area. The low abundance of red deer and elk can be explained by the unfavorable habitats for these species in the study area. Red deer prefer woody stands adjacent neighboring agriculture fields, while elk prefer pine stands (Bluzma, Baleišis, 1999), neither of which were typical to the study area.

The beaver has the ability drastically to change the structure of the plant community. In beaver wetlands in North America, beaver foraging activity encouraged the growth of successive species like willows, birches, aspens and alders instead of climax species like oaks and maples (Johnston, Naiman, 1990b; Wright *et al.*, 2002; Wright *et al.*, 2004). These changes have a positive effect on the distribution of ungulates in the landscape, especially in winter. The major proportion of winter diet of roe deer, red deer and elk consists of willow branches, and the bark of birches and aspen (Prūsaitė *et al.*, 1988; Tixier, Duncan, 1996; Shipley *et al.*, 1998; Gebert, Verheyden-Tixier, 2001). In our study area, we found a slightly higher abundance index for ungulates in beaver wetlands compared with other habitats. Also, tracks of elk were found only in plots with beaver wetlands, indicating that elk use the beaver wetlands in the area.

During the study, we noted that the majority of willow buds in beaver wetlands were freshly cut by roe deer and elk to a height of 2.5 meters. These species were identified from tracks not older than few days and teeth marks on the bark. These signs indicates the attractiveness of beaver wetlands as winter foraging habitat for elk.

The abundance of the Eurasian beaver has not changed much in Varėnė, Merkys, Šalčia, Šventoji and Virinta from 1999 to 2002 to the present. According to Ulevičius and Balčiauskas (2002), the abundance index for Eurasian beaver

varied from 15 to 22 beaver signs (cut trees, traips) per 500 m of the shore in 2002. The same segments of those rivers were studied from 2012 to 2013 and we found a slightly decreased abundance index for Eurasian beaver, but no significant differences were detected. Meanwhile, the abundance indices of other semi-aquatic mammals have significantly decreased over the 10-year period in comparison with studies carried out from 1999 to 2002 (Ulevičius 2001b; Ulevičius, Balčiauskas, 2002). According to Brzezinski *et al.* (2010), the main reason explaining the decline of muskrat was the increasing densities of American mink in Poland. Secondary factors mentioned were habitat loss, availability of food, diseases, parasitism and predation by other carnivores and raptors (Brzeziński *et al.*, 2010). The more possible reason for the decline of muskrat in Lithuanian rivers is habitat loss since the abundance indices of American mink and otter have decreased significantly in same rivers too. Little is known of the causes of the American mink decline in Europe (Bonesi, Palazon, 2007). In some mink farms in Europe, outbreaks of the Aleutian mink disease was documented and it could be, that escaped individuals have transferred the disease to free-roaming American minks (Chriél *et al.*, 2012; Knuutila *et al.*, 2015). It is possible that in other regions of Europe, the same disease has spread to natural habitats and this can account for the decrease in densities of American mink. In some rivers in Lithuania a high abundance index and high frequency of occurrence of water voles were registered. It is possible that the lower abundance of muskrats as a direct competitor, and American mink as a primary predator, have contributed to the increase in abundance of water voles in Lithuania.

The decrease of American mink and muskrat was observed only along rivers. Our observations of American mink occurrence in beaver wetlands documents that they are frequent visitors and use these habitats intensively in winter. In addition, tracks of American mink were frequent in drainage ditches in eastern Lithuania (personal observation). A similar situation was observed for muskrats where every year in 8 to 10 beaver wetlands (30 to 40 total sites), lodges

of muskrat were found (personal observation). It is possible that beaver wetlands that experience less anthropogenic pressure, and thus may be more attractive habitats to muskrats and American mink than rivers. A second reason may be that beaver wetlands have more stable water levels than rivers. According to Brzezinski *et al.* (2010), muskrats are sensitive to changes in water level. This might be one of the main factors limiting muskrat abundance in rivers. In Lithuania, high water levels were observed in rivers during the last decade, which could damage muskrat houses, flood nests, reduce plant growth and force migration to peripheral habitats (Skyrienė *et al.*, 2014).

4.3. The importance of beaver burrows to different ecological groups of mammals

The majority (67%) of the small and medium-size mammals (except bats and dormice), which are common to fragmented landscape of Lithuania (Balčiauskas *et al.*, 1999), use beaver constructed burrows.

The number of effective triggers (visiting intensity, VI) of small mammals were significantly higher than medium size carnivores. Also, the frequency of occurrence of small mammals was greater than carnivores. The bank vole and members of the *Soricidae* family were more abundant and more captured on camera more frequently than other small mammals. The bank vole is a typical generalist that could be found in all types of habitats; meanwhile shrews (such as common, water and pigmy shrews) are closely related to riparian habitats (Prūsaitė, 1988; Balčiauskas, Juškaitis, 1997). According to Ulevičius and Janulaitis (2007), the bank vole is closely related with beaver habitats. It is the most abundant small mammal caught on beaver lodges. The yellow-necked mouse was the third most common small mammal observed in beaver burrows. The majority of the beaver burrows investigated were in the forest or next to this habitat, which explains the frequent occurrence of yellow-necked mouse, which is

a forest species. Other small mammal species were rare in beaver burrows. The possible reason could be the location of the beaver burrows in the habitat or because they are rare species in Lithuania.

No habitat effect on visiting intensity of beaver burrows was found among species or among ecological groups of mammals. Some logically explainable, but statistically not significant differences among habitats were revealed. The visiting intensity of bank voles tended to be lower in drainage ditches, where the visiting intensity of the striped mouse, increased in this habitat. A possible cause for this difference may be the lower amount of forested habitat surrounding a drainage channel. For ecological groups of mammals, the differences were also inconspicuous. However, these data show that drainage ditches transformed by Eurasian beaver activity can be attractive habitats for many small and medium-sized mammals, especially American mink and martens. One of reasons for the absence of a statistically significant habitat effect can be high variation of visitation parameters among catching events, which in many cases exceeded than mean.

The most common semi-aquatic mammals, observed in beaver burrows were the American mink and the otter. It is known, that otters and mink use beaver burrows as an ice-free access to water (Sidorovich, 1992). In addition, since both species prey on small mammals (Brzeziński *et al.*, 1993; Harrington, Macdonald, 2008) it could be that the odor of small mammals using the burrows that attracts these carnivores.

Our study documents that beaver burrows are important habitats for small mammals in winter. We recorded a greater number of effective triggers per 30 days in winter than in summer. It could be that small mammals use beaver burrows during winter to avoid extremely low ambient temperatures, since the temperature inside the burrow rarely drops below 0° C (personal observation). In addition, some photos revealed that small mammals feed in beaver burrows during winter. The bank vole and the yellow-necked mouse were recorded carrying

acorns inside the beaver burrow during the warm season, which could be used during winter and a water shrew was recorded feeding on dead fish during winter. Thus, beaver burrows can function as habitats to store food for winter use. Not only small mammal use the beaver burrows for feeding. American mink was recorded feeding on amphibians in beaver burrows during winter.

The 24-hour activity of the most abundant mammal species was also investigated. The bank vole was active in beaver burrows throughout the 24-hour period both in warm and cold seasons, but the intensity of activity differed between the seasons. According to Greenwood (1978) and Wójcik and Wołk (1985), bank voles are more diurnal mammals using the day time for feeding while being less active at night in summer. Bank voles are inactive during dawn and dusk. Our results show similar patterns in beaver burrows. The activity of the bank vole increases after dawn and lasts until dusk, but sharply drops at dawn, dusk and at midnight in beaver burrows in summer. The activity is lower at night than during the day. This findings suggests that beaver burrows may be used by bank voles as a diurnal feeding habitat and as a nocturnal shelter. According to Gębczyńska (1976), the bank vole feeds on vegetative parts of plants (including roots), insects and seeds. All of these food sources were recorded in beaver burrows. In beaver burrows during the cold season, the diurnal activity pattern of the bank vole was similar to that during the warm season, but was shifted in time. Bank voles were more active before dawn, between dawn and dusk and after dusk during winter.

According to Buchalczyk (1972), shrews are active all day and have no long resting periods, which is specific to other small mammals during summer. However, the feeding and locomotion activities of shrews suggest that it is a more nocturnal than diurnal animal. The activity of shrews differs between the seasons (Buchalczyk, 1972) since they are more active at night in summer, but more active during the day in winter. In addition, according to Buchalczyk (1972), shrews are significantly more active in summer than in winter. In our case, shrew species had

no discernable activity cycle in beaver burrows in summer. They were active throughout the 24-hour period, but the activity was significantly lower compared to the cold season. This finding indicates that beaver burrows could be attractive habitats for shrews during the winter than summer. The most reasonable explanation for the attractiveness of beaver burrows is the higher temperature inside the burrow compared to outside (personal observation). During the winter, we found higher activity of shrews at night. It could be that shrews spend the colder night in the burrow and leave the burrow to hunt during the day when outside temperatures can be higher.

The yellow-necked mouse is a typical nocturnal small mammal (Wójcik, Wołk, 1985). It feeds and hides from the predators at night and rests during the day. A similar 24-hour cycle was observed for the yellow-necked mouse in beaver burrow. It visits the beaver burrow mostly at night in both warm and cold seasons. It could be that yellow-necked mouse stores food supplies and uses the burrow as a relatively safe habitat to feed. The low activity in beaver burrows during day indicates that burrows are not used as a shelter from the predators or for rest sites.

4.4. The importance of beaver lodges to small mammals

Beaver lodges are complex structures made of different sized tree fragments, mud and turf. Inside the lodge, there are beaver-made chambers, holes, ventilation shafts and cavities which are not filled with mud while building a lodge (Ulevičius, Juškaitis, 2005). Such a structure could look and function in a similar manner to ones that naturally form in the forest. For example, the root system of standing trees or microhabitats that occur around and in the stump/root system of fallen trees (Maser *et al.*, 1989). Such cavities and holes both in the forest and in beaver lodges may attract small mammals and be used as temporal shelters, feeding sites, resting sites, breeding sites and even overwintering areas (Maser *et al.*, 1989; Merrit, 2010).

The seasonal changes in trapping success of small mammals on beaver lodges were similar to studies in different habitats (Pucek *et al.*, 1993; Mažeikytė, 2002; Čepukienė, 2014). The trapping success of small mammals was lowest in spring and then increased through the summer and reached a peak in autumn. These changes are induced by the reproduction rate of small mammals, which is caused by greater availability of food sources (Pucek *et al.*, 1993) and decreased pressure of predators (Erlinge *et al.*, 1983). According to Čepukienė (2014), the relative abundance of small mammals is similar in the same habitats in winter (January) and spring (April). However, on beaver lodges, the trapping success for small mammals was greater during winter than in spring. It could be that beaver lodges become a focal point in winter and represent important overwintering habitats for small mammals. In spring, the significant decrease in trapping success of small mammals could be caused by the increased activity and predation of *Mustelids*, especially of American mink, in late winter, when the mating period begins. The following results of activity of American mink on beaver lodges in February show, that depending on the year, the frequency of occurrence of American mink on beaver lodges can reach up to 75%.

Beaver lodges are important habitats for small mammals in winter. Due to the specific structure of the lodge, a relatively stable microclimate is maintained inside. The mud on the lodge works like an insulating seal and protects the inside from extreme temperature fluctuations (Stephenson, 1969; Dyck, McArthur, 1993). Because of beaver activities inside the lodge, the temperature remains above or near freezing even if the outside temperature drops below -40°C. The temperature in abandoned beaver lodges also is relatively stable and much milder than outside due to processes of decomposition (Stephenson, 1969; Buech *et al.*, 1989; Dyck, McArthur, 1993).

Small mammals, like voles and mice, are herbivores that mainly feed on herbs and seeds in summer (Prūsaitė, 1988; Merrit, 2010). Beaver lodges can be important sites for food storage for herbivores because they are built using

different species of trees and shrubs. The fragments of wood used vary in size from large parts of the trunks to thin branches. During observations of beaver lodges in our study area during the winter season, we found various signs of feeding by small mammal species. Bite marks on thin branches of *Salix* spp, *Populus* spp, *Betula* spp, *Padus avium*, *Alnus* spp, *Frangula alnus*, *Quercus robur* were very common (more than 32.4 % of all observed lodges). This use of cut stems indicates that beaver lodges are attractive not only because of a suitable microclimate, but also because of available food. These factors allow small mammals to stay inside the lodge for the entire winter.

Beaver lodges cannot be regarded as large, extensive habitats for small mammals, like forests, but these beaver-built structures, due their limited size, may serve as important elements of the total habitat structure for small mammals. Small mammal capture rates are most likely influenced primarily by the surrounding habitat type (wetland or forest) and secondarily by within-habitat structures such as beaver lodges. However, due to their high potential as shelters and locations of food resources, beaver lodges seem to function as important survival stations for small mammals during winter, thus, influencing the local population dynamics of small mammals.

Two species of small mammals caught on beaver lodges – the bank vole and yellow-necked mouse – can be considered as typical-for-the-forest habitat specialists (Gurnell, 1985; Prūsaitė, 1988; Mazurkiewicz, 1994; Tattersall *et al.*, 2002). The common shrew, despite its high abundance and occurrence in the forest habitats, is regarded as a habitat generalist species (Prūsaitė 1988, Sundell *et al.*, 2012).

Results of our study show the bank vole being the most successful inhabitant of beaver-built structures. Overall trapping success for this species exceeded by as much as four times the trapping success of the common shrew on beaver lodges. Bank voles were also captured most often in the forest, followed by the yellow-necked mouse. The yellow-necked mouse seems to benefit from

Eurasian beaver activities only in some cases, especially in the warm season, but it was obviously less related with the beaver built structures than the bank vole.

Differences in ecological characteristics of these two species may account for observed differences in capture success. Both species inhabit similar forest habitats, but the yellow-necked mouse is more associated with mature forest habitats (Andrezejewski, Olszewski, 1963; Niethammer 1978; Gurnell 1985) since it has greater abilities to climb in the canopy and occupy tree cavities than the bank vole. In addition, the yellow-necked mouse was found closely related with crop trees in autumn since it prefers to feed on highly energetic seeds of oak, hazel, and other species (Juškaitis, 2002). Winter food caches of the yellow-necked mouse, consisting of these seeds, were quite common in nest boxes of birds and dormice (Juškaitis, 2010). The bank vole illustrates far less climbing ability and basically feeds on small seeds, green parts of plants and bark (Niethammer, Krapp, 1982; Prūsaitė, 1988). These food categories are available on beaver lodges throughout the year. During the growing season, the beaver lodges are overgrown by herbs and shrubs of various species (Griazina, 2011; Obidziński *et al.*, 2011) that produce seeds which could be consumed by bank voles. During winter, bank voles feed on the bark of trees and shrubs, which were used by beavers rebuilding and renovating the lodge in autumn.

Living sympatrically, the bank vole and the yellow-necked mouse may compete for resources which then leads to microhabitat partitioning and niche segregation (Hille, Mortelliti, 2010). Under conditions of high densities, the physically stronger yellow-necked mouse may force the weaker bank vole from optimal microhabitat (Andrezejewski, Olszewski, 1963; Wójcik, Wolk, 1985). Our data on trapping success and frequencies of occurrence on beaver lodges indirectly do not confirm interference competition between these two species, probably because beaver lodges may be more optimal microhabitats for the bank vole than for the yellow-necked mouse. In our study, the bank vole showed significantly higher trapping success on beaver lodges than in the forest in autumn

and winter, while the yellow-necked mouse was trapped more successfully in the forest in autumn and absent on beaver lodges in winter. Moreover, the bank vole showed relatively low multiannual variation in trapping success on beaver lodges indicating stable occupation of this microhabitat over multiple years.

The bank vole tends to inhabit sites with well-developed undergrowth and abundant hiding places within coarse woody debris. Moreover, this species is reported to prefer wet forest habitats (Mazurkiewicz, Rajska-Jurgiel 1987). The habitat humidity factor even shaped the distribution of bank vole in southern parts of the species distribution range (Torre, Arrizabalaga, 2008). These habitat features are rather common on beaver lodges and in their surrounding environments.

The common shrew showed obvious preference for beaver lodges over the forest habitat during all seasons. This species feeds almost exclusively on animals, mainly insects, worms and snails that live in the surface layer of the soil (Churchfield, 1982; Prūsaitė, 1988; Hutterer *et al.*, 2008). Shrews prefer cool, damp and shady habitats with dense vegetation, such as riparian forests and reed beds (Hausser *et al.* 1990), which is similar to beaver lodge environments. Common shrews had a lower trapping success rate than bank voles on beaver lodges. This lower success rate can best be explained not by microhabitat selectivity differences between these species, but rather by behavioural differences. Common shrews are strongly territorial and their densities are naturally lower than densities of other small rodents (Nosek *et al.*, 1972). The other two species of shrews – pigmy shrew and water shrew – were rarely found on beaver lodges, probably due their overall rarity in Lithuania in comparison with common shrews (Balčiauskas *et al.*, 1999).

The short-tailed vole occurs in a wide range of habitats including grasslands, woods, upland heaths, dunes, marshes, peat-bogs and river-banks, and tend to prefer damp areas (Kryštufek *et al.*, 2008). However, being a habitat generalist, at the same time it is defined as a relative feeding specialist requiring

highly caloric food. This requirement can cause high intraspecific competition among individuals and may lead to relatively low local densities of short-tailed voles (Myllymäki, 1977b). Despite low trapping success and occurrence on beaver lodges, short-tailed voles were more common in this habitat than in the forest. On beaver lodges they were found in all seasons, whereas in the forest only during spring.

Individuals of the remaining seven species caught during our study contributed to the small mammal community structure on beaver lodges, but not in the forest. The proportion of these species in the small mammal community increased during autumn on beaver lodges, probably because of greater overall abundance of small mammals during this season. Beaver sites, not just lodges, represent potential habitats for these species. The wetland environments of beaver sites vary in size, but in some cases can form quite extensive areas covering several hectares (Ulevičius *et al.* in prep.).

Generally, our data show that small mammal species richness and community structure on beaver lodges can be influenced by the surrounding habitats – mainly by the forest and probably less by other habitats. Individuals of the bank vole represent about 60 to 80% of the small mammal community in Lithuania's forests (Balčiauskas, Juškaitis, 1997; Šinkūnas, Balčiauskas, 2005). This finding is similar to the structure of the small mammal community on beaver lodges found during this research.

4.5. The demographic parameters of small mammals occupying beaver sites

The age structure of small mammal populations is determined mainly by the inner mechanisms of population changes and less by the density of the predators, available food, and characteristics of the habitat (Krebs, Myers, 1974; Oli, Dobson, 2001). At northern latitudes, the age structure observed in small

mammal populations also is affected by season (Krebs, Myers, 1974; Hansson, 1978). According to Prūsaitė (1988), adult female bank voles may account for up to 100% of all captured females in early spring because the individuals mature over the winter. The frequency of adults in a population decreases from the spring to October due to the presence of newborns. One mature female bank vole may produce an average of 5 offspring 1 to 4 times per year. By late autumn, the ratio of adult individuals increases again due to mortality of late summer juveniles and the maturity of offspring from late spring and early summer. In our study area, similar patterns of seasonal dynamics in age structure for bank voles were observed. The frequency of adults was highest in spring and decreased from summer until the winter in all studied habitats, while the frequency of non-reproducing individuals increased at the same time and reached a peak in winter.

The phase of a population cycle may impact the sex ratio of small mammal populations. The sex ratio in a normal density small mammal population should be close to 1:1 (male to female) (Krebs, Myers, 1974). According to Myllymäki (1977b), high/low densities of animals distort the sex ratio in cyclic populations in northern Sweden. For example, at the peak of the population cycle for field voles the sex ratio of adult animals was close to 1:1 at the start of the breeding season. In a dense population in July, the sex ratio was heavily biased towards adult females and was still increasing through the autumn (Myllymäki, 1977b). Hansson (1978) reported this same pattern in field voles. However, Hansson (1978) found that changes in the sex ratio of bank voles are not the cause of the rodent cycles. Based on these studies we believe that the sex ratio of bank voles in our area should be 1:1 and the observed deviations from the equilibrium are caused by other factors.

On beaver lodges and in the forest control habitats, we found the sex ratio of the bank vole to be close to 1:1 and it did not vary significantly among the seasons. However, we did observe seasonal changes in the sex ratio of adults captured on beaver lodges. This deviation from the expected 1:1 ratio may be

caused by differing mobility behavior between adult males and females. According to some authors, adult males of bank voles have larger home ranges than females (Norrdahl, Korpimaki, 1998; Kozakiewicz *et al.*, 2007). The increased mobility caused by a larger home range could increase the probability of adult males being captured.

4.6. The helminthological parameters of two small mammal species occupying beaver sites

We did not identify substantial differences of small rodent infection levels by helminths between beaver sites and the forest. Statistically significant differences were found only in specific solitary aspects of infection.

Helminth species composition fully overlapped in two tested habitats for the bank vole (8 species of parasites in bank voles in each habitat) and was very similar for the yellow-necked mouse (7 species in beaver sites and 6 species in the forest).

Analysis of specific helminth species documented only one, *Syphacia petruszewiczi*, as being significantly more abundant in bank voles occupying beaver sites than in the bank voles occupying forest habitat. No statistically significant differences were found for any helminths parasitizing the yellow-necked mouse occupying the different habitats.

In both small rodent species, a slightly lower number of helminth species and other taxa was found during our research (8 species or other taxa for bank vole and 7 – for yellow-necked mouse). For all of Lithuania (at a larger regional scale), more than 20 helminth species have been described parasitizing the bank vole and 10 helminth species found in the yellow-necked mouse (Prūsaitė 1988) and 42 helminth species/taxa in the bank vole and 17 in yellow-necked mouse, respectively (Mažeika, 1992). However, at a local scale findings can be somewhat lower. In a mountain locality of Serbia, the bank vole was reported to be infected

by seven species of nematodes (Bjelić-Čabrilo et al., 2009), and eleven species of helminths were found infecting bank voles in three localities in northern Poland (Behnke et al. 2001). Similar helminth species numbers were reported for yellow-necked mouse in a local territory in Germany (Klimpel et al., 2006). In our research, since the helminth species were the same or nearly the same in two tested habitats for the bank vole and for the yellow-necked mouse, it suggests that the species composition of a helminth community in small rodents at the local scale is not affected by the habitat.

Different species of parasites were sometimes characterized by the contrary patterns of rodent infection in both tested habitats. For example, the most pronounced differences in infection level (prevalence of infection) of the bank vole by two different species of helminths (*Syphacia petruszewiczi* and *Heligmosomum mixtum*) were controversial between the two habitats. It might be expected that these parasite species have different habitat requirements when infecting the same host species since the crucial factor for reproductive success is humidity for some species of *Syphacia*, while temperature is critical for *Heligmosomum mixtum* (Определитель ..., 1979; Haukisalmi, Henttonen, 1999).

In other studies, the bank vole infection levels by these two parasites were found to be also controversial in similar habitats but from different neighboring localities (Behnke, et al., 2001, Kuliś-Małkowska, 2007). This may indicate probable intrinsic (age, sex), extrinsic (time, season) factors in both the parasites and the host populations, as well as synergistic and antagonistic interactions between parasite species (Ferrari et al., 2003; Ferrari et al., 2004; Behnke et al., 2005; Kuliś-Małkowska, 2007).

We found changes in the helminth community structure (expressed by abundance of helminth species) between the two studied habitats for two species of small rodents. Generally, *Syphacia petruszewiczi* strongly dominated the other helminth species in bank voles at beaver sites, whereas in the forest the presence of this helminth was much lower. In the yellow-necked mouse, we found

completely different dominant species between two habitats. *Syphacia montana* was the strong dominant at beaver sites, but not found in mice dwelling in the forest, where *Syphacia stroma* was dominant.

The dominance of one species in a helminth community is a commonly reported phenomenon and usually one or a few species dominate over many other species parasitizing at low abundance levels (Poulin *et al.*, 2008). The occurrence of a helminth species may be influenced by abiotic factors affecting the intermediate hosts (Krasnov *et al.*, 2008), and different patterns of helminth domination can be explained by peculiarities of life cycles of the helminth species in different habitats.

The helminth community diversity indices varied considerably among seasons. However, we cannot find any regularity in these seasonal patterns that would logically explain differences between habitats. This differences suggest that the parasite diversity is varying by a chance in both habitats.

Our findings did not discover obvious differences in parasite distribution among host individuals between two tested habitats. Parasite distribution among host individuals is determined by many factors (Anderson, Gordon, 1982). In our study, helminths in the bank vole and the yellow-necked mouse showed an aggregate distribution in a host population, similar to that found by other researchers (Haukisalmi, Henttonen, 1999). The reasons for the aggregated distribution are not exactly known and can be varied: 1) it is important whether helminths contacted the host earlier or not, 2) the social status of individuals in a group, 3) infection with other helminths, 4) host and parasite genetics, 5) host diet, 6) host behavior, and additional specific factors (Anderson, 1991). Parasites in small rodents are characterized by the aggregate distribution in host populations, which is considered one of the stabilizing factors of the host-parasite interactions (May, Anderson, 1978, Wakelin, 1987). In addition, the aggregate distribution of helminths can reduce interactions among helminths (Wakelin, 1987).

Among the special findings from our research, we would like to highlight the case of *Hydatigera taeniaeformis*, which was found in the larvae stage (*strabilocercus fasciolaris*) in the bank vole. This finding suggests that if an infected bank vole is eaten by a higher trophic level animal it would be infected with this helminth. According to Козлов (1977), this helminth does parasitize carnivorous mammals, and can be found in humans as well. The intermediate host of *Hydatigera taeniaeformis* is usually a rodent (Козлов, 1977). In Lithuania this helminth was also found in *Mus musculus*, *Apodemus agrarius*, *A. flavicollis*, *Microtus arvalis*, *Rattus norvegicus* in Kėdainiai district and Vilnius suburbs (Mažeika, 1992) and in *Ondatra zibethicus* in Rusnė Island (Mažeika *et al.*, 2009). We did not find any differences in the bank vole infection levels by this parasite between the two tested habitats. Thus, beaver sites cannot be regarded as more risky habitats than forests for human health and for predators with respect of *Hydatigera taeniaeformis* infection.

Examining the total infection of rodents regardless helminth species (all helminth species combined together), the forest might be considered as more optimal habitat than the disturbed environments of beaver sites for at least the bank vole. This finding is based on differences in total mean abundance of parasites, which was significantly higher in this rodent species in beaver sites in winter. For the yellow-necked mouse we have observed only statistically insignificant tendencies of higher abundance of parasites in beaver sites, with these tendencies being more clearly pronounced in autumn. Helminth infection prevalence in these rodent species has also revealed a few and controversial significant differences between habitats (only for bank vole) among particular species of parasites, and no differences when all helminth species were considered together.

CONCLUSIONS

1. The Eurasian beaver has significantly affected the habitat structure of the hilly morainic landscape in eastern Lithuania by creating the beaver wetlands, which include many specific elements of habitat infrastructure: lodges, burrows, dams, dead wood and channels. The area of beaver wetlands comprised from 9.05% to 12.43% of the whole study area. The average size of a beaver wetland is 3.97 ha (range from 0.09 to 47.97 ha). The lengths of beaver wetland/forest and beaver wetland/open area ecotones comprised 20.4% and 23.1% of the length of all ecotones in the study area, respectively.
2. Quantification of beaver impacts on the habitat structure using remote *ex situ* mapping has led to underestimations in the beaver wetland area, especially those under the tree cover. A correction factor developed through *in situ* mapping allowed to us to improve the precision of quantification. The coefficient of 1.2 was found to be best for correcting *ex situ* and *in situ* discrepancies.
3. The abundance indices (AI) and diversity of large and mid-sized mammals in beaver-affected habitats were found to be similar in comparison to other habitats in the study area. The most abundant species in the beaver wetlands were *Capreolus capreolus* (AI=1.12) and *Vulpes vulpes* (AI=1.15), species that are typical to fragmented landscape. The total average AI of large and mid-size mammals in beaver sites (AI=3.38) was higher than in the other habitats, but significant differences were found only between beaver sites and open area habitats (AI=1.83) and beaver sites and mosaic habitats (AI=2.16) (Mann-Whitney: $p < 0.001$ and $p = 0.001$, respectively). The diversity of large and mid-size mammals at beaver sites ($H' = 2.351$) was similar to the forest ($H' = 2.551$), open habitats ($H' = 2.378$) and mosaic habitats ($H' = 2.581$).
4. Seventeen species (or other taxa) of mid-sized and small mammals were documented inside burrows of beavers using the IR camera trap method.

Mainly mammals of two ecological groups were found: small mammals (*Clethrionomys glareolus*, Soricidae, *Apodemus flavicollis*, *A. agrarius*, *Arvicola terrestris*), and carnivores (*Neovison vison*, *Martes* spp., *Lutra lutra*, *Mustela putorius*, *Nyctereutes procyonoides*). *Clethrionomys glareolus* was absolute dominant among all taxa with average visiting intensity and frequency of occurrence (VI, effective triggers of IR camera/30 days; FO, %) (VI=41.73; FO=100%). *Neovison vison* dominated among carnivores (VI=1.7; FO=84%). Some mammals showed significantly lower visiting intensity (VI<0.1). These included *Mustela* spp., *Meles meles*, *Vulpes vulpes*, *Ondatra zibethicus*, *Talpa europaea*, *Sciurus vulgaris*, and *Castor fiber* itself.

5. The effect of seasons was more pronounced than the effect of the beaver site type to the visiting intensity of mammals in beaver burrows. This is particularly evident for small mammals (Mann-Whitney test: $df=35$, $p=0.007$) and shrews (Mann-Whitney test: $df=35$, $p=0.009$). For the most common visitors (*Clethrionomys glareolus*, *Sorex* spp., *Apodemus flavicollis* and *Neovison vison*) of beaver burrows, the 24-hour activity was significantly higher in cold season than in warm season.
6. Small mammals of eleven species were caught on beaver lodges using snap traps. *Clethrionomys glareolus* was the dominant species in terms of trapping success (TS=47.5 inds/100 trap-nights), while *Sorex araneus* (TS=11.86) and *Apodemus flavicollis* (TS=4.7) were the subdominants. In the forest, five species were captured with the bank vole most abundant (TS=29.43) and the yellow-necked mouse next most captured (TS=9.87). The trapping success of small mammals on beaver lodges was greater than in the forest in all seasons, but significant differences only were found in autumn (Mann-Whitney: $p<0.05$). The Shannon diversity index of the small mammal community on beaver lodges was similar to that in the forest in all seasons. However, the community structure of small mammals on the beaver lodges was different from that in the forest. The greatest differences between the small mammal

communities in these habitats were found in summer (χ^2 - test; $df=4$, $p<0.001$), autumn (χ^2 test; $df=4$, $p=0.001$) and in winter (χ^2 test; $df=4$, $p=0.004$) and was caused by different proportions of the subdominant *Apodemus flavicollis* (higher in the forest) and *Sorex araneus* (higher on beaver lodges).

7. Beaver alterations of habitat infrastructure revealed a rather weak influence on the demographic characteristics of the dominant small mammal species, *Clethrionomys glareolus*. The age structure and the sex ratio of *Clethrionomys glareolus* on beaver lodges was similar in comparison to the forest in all seasons.
8. Occupation of beaver-transformed environments by the two small mammal species, *Clethrionomys glareolus* and *Apodemus flavicollis*, typically found in the forest did not lead to significant changes of their helminthological status, although variation among parasite species and seasonal variation were found. *Clethrionomys glareolus* was infected with the same eight species of helminths in beaver sites and in the forest. The mean infection rate in beaver sites was similar to that in the forest. In *Clethrionomys glareolus* only one helminth species *Syphacia petruszewiczi* was more abundant in beaver sites than in the forest (Mann-Whitney: $p<0.001$). *Apodemus flavicollis* were infected by seven helminth species (or other taxa) in beaver sites and six in the forest. The nematode *Syphacia montana* was found only in mice dwelling in beaver sites. Total mean abundance of all parasites in *Clethrionomys glareolus* showed higher infection levels of this rodent in beaver sites than in the forest in winter (Mann-Whitney test: $p = 0.049$).

The publication list of the author (2011-2015)

The publication in the list of Thompsons Reuters Web of Knowledge (ISI):

1. Skyrienė G., Ulevičius A., **Samas A.** 2011. Levels of helminth infection of small rodents in two interspersed habitats – forest and beaver sites. *Baltic forestry*, Vol. 17, No. 2: 299-307.
2. **Samas A.**, Ulevičius A. 2015. Beaver building activity favors the typical-for-the-forest small mammals. *Baltic forestry*, Vol. 21, No. 2: 244-252.

The publications in other peer-reviewed journals:

1. Skyrienė G., Paulauskas A., Ulevičius A., **Samas A.** 2014. Decline of invasive muskrat in Lithuania. *Вестник охотоведения (Game Management Issues)*, Vol. 11, No. 2: 291-295.
2. Ulevičius A., **Samas A.**, Prankaitė T. 2015. Camera traps in beaver burrows: monitoring of species diversity, habitat and season effects. *Beiträge zur Jagd- und Wildforschung*, Bd. 40: 201-210.

Conference thesis:

1. **Samas A.**, Ulevičius A. 2009. Small mammal community structure and demographic parameters of their population in beaver sites. 5th International Beaver Symposium, Dubingiai, Lithuania, 20-23 September, 2009 (ISBN: 9789955125075).
2. Butautytė G., **Samas A.**, Ulevičius A. 2009. Parasitological research on small mammals dwelling in beaver sites. 5th International Beaver Symposium, Dubingiai, Lithuania, 20-23 September, 2009 (ISBN: 9789955125075).
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AKNOWELEDGEMENT

First of all, I would like to express my gratitude to my supervisor dr. Rimvydas Juškaitis and my scientific consultant dr. Alius Ulevičius for advices writing the PhD thesis, for help during the expedition and collecting the study material, for enthusiasm and ever-friendly nature.

I also wish to sincerely thank to my reviewers habil. dr. Linas Balčiauskas and prof. dr. Jana Radzijeuskaja for deeper view into the PhD thesis and for constructive remarks.

I wish to acknowledge the support received from Peter Busher, Boston Massachusetts. His ideas and remarks were very helpful writing the PhD thesis.

I would like to thank the scientific team of the Center of Ecological and Environmental Science of Faculty of Natural science, Vilnius University for the patience.

I also would like to thank the Research Council of Lithuania for the financial support (LEK-14/2012 and DOK-14297).

I am very grateful to my future wife and my family for the support at difficult times.

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ANNEXES

Annex 1. List of Lithuanian rivers where the study of abundance and occurrence of semi aquatic mammals was carried out in 2012-2013.

No.	River	Belongs to basin of	No.	River	Belongs to basin of
1	Nemunas, Atmata	Baltic sea	35	Daugyvenė	Mūša
2	Minija, lower course	Nemunas	36	Beržtalys	Lielupė
3	Danė	Baltic sea	37	Lievuo	Mūša
4	Šyša, upper course	Nemunas	38	Lėvuo	Mūša
5	Tenenys, upper course	Minija	39	Pyvesa	Mūša
6	Veiviržis	Minija	40	Apasčia	Nemunėlis
7	Minija	Nemunas	41	Apasčia	Nemunėlis
8	Salanta	Minija	42	Nemunėlis	Lielupė
9	Varduva	Venta	43	Nevėžis	Nemunas
10	Venta	Baltic sea	44	Šventoji	Neris
11	Sruoja	Varduva	45	Šventoji	Neris
12	Virvyčia	Venta	46	Šventoji	Neris
13	Venta	Baltic sea	47	Siesartis	Šventoji
14	Venta	Baltic sea	48	Virinta	Šventoji
15	Venta	Baltic sea	49	Vyžuona	Šventoji
16	Dabikinė	Venta	50	Jara	Šventoji
17	Jūra	Nemunas	51	Šetekšna	Šventoji
18	Jūra	Nemunas	52	Dysna	Dauguva
19	Jūra	Nemunas	53	Žeimena	Neris
20	Aitra	Jūra	54	Žeimena	Neris
21	Ančia	Jūra	55	Lakaja	Žeimena
22	Šešuvis	Jūra	56	Mera	Žeimena
23	Šlyva	Šaltuona	57	Strėva	Nemunas
24	Nemunas	Baltic sea	58	Strėva	Nemunas
25	Mituva	Nemunas	59	Verknė	Nemunas
26	Alsa	Mituva	60	Verknė	Nemunas
27	Nemunas	Baltic sea	61	Nemunas	Baltic Sea
28	Dubysa	Nemunas	62	Merkys	Nemunas
29	Dubysa	Nemunas	63	Skrobla	Merkys
30	Luknė	Dubysa	64	Ūla	Merkys
31	Dubysa	Nemunas	65	Varėnė	Merkys
32	Kražantė	Dubysa	66	Merkys	Nemunas
33	Švėtė	Lielupė	67	Šalčia	Merkys
34	Mūša	Baltic sea	68	Visinčia	Šalčia
			69	Merkys	Nemunas