Eurasian Beaver Building Activity Favours Small Mammals Common for the Forest

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Abstract

Beaver-built structures, such as beaver lodges, can be regarded as specific environment infrastructure components that are supposed to be important to a number of species due their morphological, topographical, microclimate, and temporal features. We have compared the species composition and trapping success of small mammals as well as inter-annual and seasonal variation of these parameters on beaver lodges and in the forest to find out the significance of beaver lodges for small mammals common for the forest. The forest proximity factor was also tested on influence on trapping success of these mammals. The study was carried in hilly landscape of Eastern Lithuania in 2007 – 2012. The mean density of beaver sites was 20 pcs. per 1,000 ha. Small mammals were sampled using snap traps on beaver lodges and in the forest once in a season four times a year.

Small mammals of eleven species were caught on beaver lodges (Shannon's H' = 1.14) and small mammals of 5 species in the forest (Shannon's H' = 0.74). The typical for the forest bank vole (*Clethrionomys glareolus*) significantly prevailed over other species on beaver lodges. The stenotopic yellow-necked mouse (*Apodemus flavicollis*) and eurytopic common shrew (*Sorex araneus*) were the subdominants on beaver lodges. The trapping success of small mammals on beaver lodges and in the forest has increased from spring to autumn with some depression in winter. In summer, autumn and winter, the overall trapping success of small mammals was significantly higher on beaver lodges than in the forest. This was also true for bank vole and common shrew but not for yellow-necked mouse, which was more successfully trapped in the forest in all seasons. Inter-annual variation of trapping success of small mammals was more expressed in winter in both habitats. Common shrew and yellow-necked mouse showed higher inter-annual variation on beaver lodges, whereas bank vole – in the forest. In autumn, the trapping success of small mammals of three species on beaver lodges was not statistically significantly influenced by the forest proximity factor. However, for the bank vole, the negative correlation between the trapping success and the forest proximity was more clearly expressed and being close to the significance level ($p = 0.055$).

Key words: Beaver lodges, forest habitat, small mammals, *Castor fiber*, *Clethrionomys glareolus*, *Apodemus flavicollis*, *Sorex araneus*

Introduction

In the majority of the researches and publications about the ecological role of the beaver, the basic attention is accented for a role of dams and ponds constructed by beavers. The other infrastructure elements (beaver lodges and burrows) created by beaver are less investigated and not much is known of the importance of these elements to biota.

Beaver-built structures, such as beaver lodges, can be regarded as specific environment infrastructure components that are supposed to be important to a number of species due their morphological, topographical, microclimate and temporal features (Барабаш-Никифоров 1950, 1959, Dyck and MacArthur 1993, Ulevičius and Janulaitis 2007). Earlier investigations in some beaver populations in Russia showed the importance of beaver burrows as shelters for more than 20 species of small vertebrates (mammals, reptiles and amphibians) (Барабаш-Никифоров 1950). Small mammals can benefit from beaver activities in different environments (Suzuki and McComb 2004, Ulevičius and Janulaitis 2007, Sidorovich 2011). However, parameters of small mammal community were not compared on beaver built structures, namely on beaver lodges, and in the surrounding habitats.

Beavers densely inhabit fragmented landscape ecosystems with tightly interspersed forest, wetland and field mosaic (Ulevičius et al. 2009). Therefore, the species composition of small mammals using beaver lodges may be influenced by surrounding habitats. Forest habitats suffer the most intensive fragmentation due the anthropogenic press, agricultural tendencies, etc. Beaver activities contribute to the habitat diversity of such areas by extending quantity of wetlands, shrubby environment and ecotone habitats.

Usually beaver sites are spatially tightly related to the forest habitat (Ulevičius et al. 2011), thus potentially making an opportunity to be inhabited by the typical forest species.

In a dense beaver population of Lithuania, ca. 60 % of beaver sites contain beaver lodges and ca. 90 % - beaver burrows. The mean density of beaver burrows in the land reclamation canals in Lithuania is 36.4 burrows/km (Ulevičius et al. 2009). The beaver burrow is a temporary structure that often collapses if is unused for one or two years and creates a micro relief with various sizes of holes and caves. Meanwhile majority of beaver lodges persist for more than 10 years, thus, being quite permanent structures of environment.

Earlier investigations of small mammals on beaver lodges (Ulevičius and Janulaitis 2007) have revealed a number of small mammal species inhabiting these structures of environment with clear domination of bank vole and yellow-necked mouse, the species that are common for the forest habitat. These findings encouraged us to fulfill a comparative analysis: the main attention was paid to comparison of the studied parameters between beaver lodges and the forest habitat. For this purpose we have included control samples from the forest habitat, extended catching events to winter season, and tested influence of the forest proximity factor on trapping success of dominating small mammals. Thus, the main goal of the present paper was to evaluate the significance of beaver lodges as the specific environment infrastructure elements for small mammals that are common for the forest and for small mammals coming from other habitats. We have studied the species composition, trapping success, community structure of small mammals on beaver lodges and in the forest habitat in a hilly fragmented landscape of Eastern Lithuania. We compared the interannual and seasonal variation of studied parameters between beaver lodges and the forest. Influence of the forest proximity on trapping success of dominating small mammals on beaver lodges was evaluated.

Material and Methods

Study area

Studies were carried out in the eastern part of Lithuania, in Vilnius, Molėtai and Širvintos districts (Figure 1). The geographic co-ordinates of the approximate center of this territory was 55°00' N, 25°14' E.

Highly moraine landscape with numerous lakes is characteristic of this territory. Mixed forests of *Picea abies, Betula* spp. and *Alnus* spp. covers about 28 % of the study area. Abandoned agricultural fields and pastures overgrown with the woodlands of early succession stages are specific to most of the open area. Only a small part of the territory is used for agriculture. Various lowlands with lakes, swamps, bogs, drainage canals and small streams take up to 25 % of the landscape (Basalykas 1977). These depressions are overgrown with *Salix* spp. and *Betula* spp., which attract beavers. The abundance of the beavers in the study area was about 20 beaver sites per 1,000 ha.

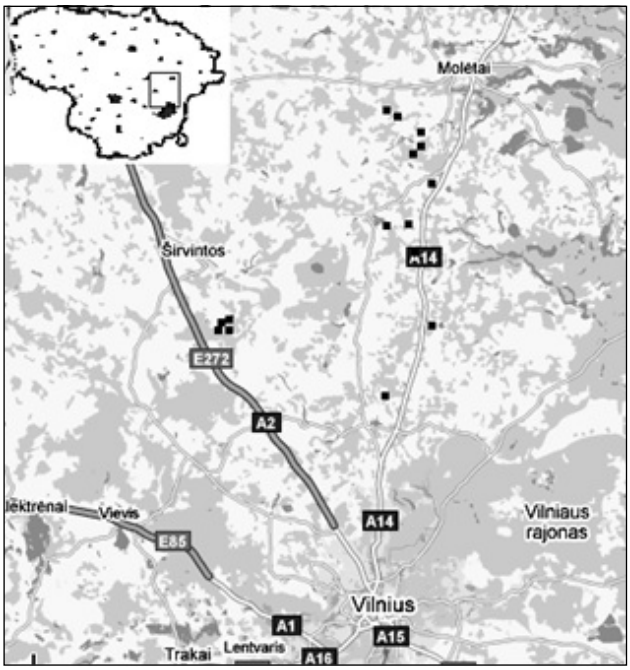

Figure 1. Study area. Small mammal trapping sites (black dots). Grey area shows the characteristic pattern of the forest fragmentation in the study area

Methods

Definition "small mammals" is used to describe the group of mammal species caught with snap-traps set on the ground surface. There are over 20 mammal species of insectivores and rodents in Lithuania assigned to this group (Prūsaitė 1988, Balčiauskas and Juškaitis 1997). About 15 species of small mammal could be found in the forest but only 3 of them: common shrew (*Sorex araneus*), yellow-necked mouse (*Apodemus flavicollis*) and bank vole (*Clethrionomys glareolus*) are common to this biotope (Prūsaitė 1988). Such species like dormice (*Muscardinus avellanarius, Eliomys quercinus, Driomys nitedula, Glis glis*) are typical forest species, but they are studied using specific methods since are living not only on the ground but also in the canopy.

Small mammals were sampled in the forest and on beaver lodges from 2007 to 2011 four times a year: in spring (April), in summer (August), in autumn (Octo-

ber) and in winter (February). To catch the animals snap traps were used. Traps were set in a quadrate of five snap traps (one in the middle of the quadrate and four in the corners approximately 5 × 5 meters) both in the forest and on the beaver lodges (Figure 2). In case of thick snow cover in winter, snap traps were placed on bare ground after snow was removed from the ground, therefore, 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 other four traps – around the base of a lodge. Small piece of brown bread crust moistened with sunflower oil were used as bait. Traps were set for three days and checked once a day. Sampling in a trap quadrate on a lodge or forest for three days was defined as one catching event and considered as one element of a sample. Sampling of small mammals by snap traps were permitted by the Ministry of Environment (license No. (11-)-D8-3650).

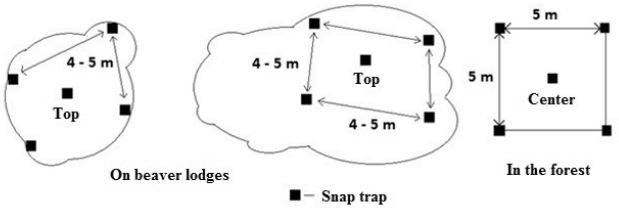

Figure 2. Snap trap placing schema on beaver lodges and in the control habitat of the forest

1,252 individuals of eleven small mammal species were caught during the studies. Differences of dental morphology of *Microtus* spp. were used to determine the species (Niethammer and Krapp 1982; Prūsaitė 1988).

Trapping success (TS) of small mammals was expressed as a standardized number of animals caught per 100 trap nights. We use the "trapping success" definition instead of standard "relative abundance" (Balčiauskas 2004), because beaver lodges are habitats of very limited size and number of trapped mammals may be highly influenced by immigrated specimens. Thus, the number of mammals trapped on beaver lodges during a catching event does not necessary reflects abundance of small mammals on a beaver lodge at a time, but possibly an immigration intensity from a surrounded habitat. The same trap placing we used also for the forest habitat to make the data comparable.

Shannon's biodiversity index (with logarithm base 2) was used to estimate small mammal diversity in different habitats (Shannon 1949, May 1975). Data on TS in majority of samples failed the normality test (Shapiro-Wilks test was used), thus, significance of differences in trapping success of small mammals was tested using the nonparametric Mann-Whitney and Kruskal-Wallis tests for pairwise and multiple comparisons, respectively (Gotelli and Ellison 2013). Relationship of the trapping success of three dominating small mammals with the distance to the nearest forest was provided only for autumn, the season of highest TS of small mammals. using the Spearman rank correlation test.

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

Structure of the small mammal community was defined as a percentage of individuals of a certain species or species group of the total number of individuals. The most successfully trapped 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 occurred species were pulled together ("other species"). Seasonal differences in community structure were tested using the Yates' χ^2 test.

Results

Species composition, trapping success and frequency of occurrence

Totally, small mammals of eleven species were caught on beaver lodges and small mammals of five species in the forest during the research period (Table 1). The most successfully trapped species in both habitats was the bank vole (*Clethrionomys glareolus*). On beaver lodges, the bank vole was followed by the common shrew (*Sorex araneus*) and the yellow-necked mouse (*Apodemus flavicollis*). In the forest, these last two subdominant species were interchanged: the yel-

Table 1. Trapping success (TS) and frequency of occurrence (FO) of small mammals on beaver lodges and the forest during the research period 2007–2011

Species	Beaver lodges, n*=180		Forest, n=150	
	TS±*SD***	FO, %	TS±*SD**	FO, %
Clethrionomys glareolus	12.15±14.87	58.89	8.54±9.79	57.62
Sorex araneus	2.96±6.47	28.89	0.41±1.45	5.30
Apodemus flavicollis	1.16±3.87	11.11	3.74±7.98	27.81
Microtus agrestis	0.9±3.91	8.33	0.05±0.57	0.70
A. agrarius	0.33±1.9	3.89	-	-
Neomys fodiens	0.22±1.39	2.78	-	-
M. oeconomus	0.22±1.39	2.78	-	-
S. minutus	0.07±0.7	1.11	0.05±0.57	0.70
M. arvalis	0.07±0.7	1.11	-	-
Mus musculus	0.04±0.5	0.56	-	-
Micromys minutus	0.04±0.5	0.56	-	-
Totally for small mammal community	18.22±18.87	72.22	12.79±12.93	66.89

* sample size (number of trapping events)
** standard deviation

low-necked mouse was more successfully trapped than the common shrew.

The micromammals of three mentioned species showed also the highest frequencies of occurrence in both habitats. Additionally, the short-tailed vole (*Microtus agrestis*) was relatively common on beaver lodges but rarely caught in the forest. The rest of species showed low trapping success and occurrence on beaver lodges and were not caught in the forest (except the rarely detected harvest mouse) (Table 1). In all species and in both habitats, the trapping success was very variable and the standard deviation was higher than the mean, which indicates a number of factors influencing this parameter.

Seasonally, the most expressed differences in TS between beaver lodges and the forest were found in common shrew (Table 2). In three seasons, summer, autumn and winter, common shrews were significantly more abundant on beaver lodges than in the forest, especially in winter. Nevertheless, the bank vole has showed the highest overall abundances, differences in TS of this species between habitats were not so obvious in any of seasons. Despite slightly higher TS of bank vole on beaver lodges than in the forest in all seasons, statistically significant differences between habitats were found only in autumn. In winter this difference was close to the confidence level (Mann-Whitney test: $p = 0.06$). The yellow-necked mouse was the third species by TS; however, it showed opposite tendencies between habitats: in 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 TS of small mammal community was greater on beaver lodges than in the forest in all seasons but statistically significant differences were observed only in autumn and in winter.

Species diversity of small mammals was greater on beaver lodges than in the forest in all seasons especially in summer (Table 2).

Inter-annual variation

We have found some significant differences in the TS of small mammals among years (Table 3). Especially this was characteristic of the forest in winter, where two dominant species (bank vole and yellow-necked mouse) differed significantly among years. On beaver lodges, multiannual differences in RA were of somewhat less extent. Here, the dominant bank vole showed significant differences only in winter, common shrew only in autumn and yellow-necked mouse only in summer. The total TS of small mammal community differed in winter on beaver lodges, whereas in the forest – in autumn and winter. The post hoc Mann-

Table 2. Trapping success (TS) and diversity of small mammal on beaver lodges and in the forest in different seasons in 2007-2011. Statistically significant differences are 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
Clethrionomys glareolus	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	
Sorex araneus	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**	
Apodemus flavicollis	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	
Microtus agrestis	0.3±0.67	0.17±36	2,13±2.23	0	0.99±0.92	0	0.16±0.15	0
A. agrarius	0.15±0.33	0	0.15±0.32	0	0.99±1.13	0	0	0
Neomys fodiens	0	0	0.28±0.45	0	0.43±0.72	0	0.16±0.15	0
M. oeconomus	0	0	0.28±0.45	0	0.43±0.72	0	0.16±0.15	0
S. minutus	0	0	0	0	0.28±0.45	0.17±0.36	0	0
M. arvalis	0	0	0.14±0.32	0	0.14±0.32	0	0	0
Mus musculus	0	0	0.14±0.32	0	0	0	0	0
Micromys minutus	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	
Shannon diversity index	1.044	0.847	1.656	0.734	1.377	1.234	1.267	0.841

* sample size (number of trapping events)

Table 3. Significance of differences in the trapping success (TS) of small mammals on beaver lodges and in the forest among years (2007-2010)

Species	Differences of TS among years on beaver lodges, Kruskal-Wallis test				Differences of TS among years in the forest, Kruskal-Wallis test			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Sorex araneus	n. s.	n. s.	p=0.004	n.s.	-	n. s.	n. s.	n. s.
Apodemus flavicollis	n.s.	p=0.03	n.s.	-	n. s.	n. s.	n. s.	p=0.03
Clethrionomys glareolus	n. s.	n. s.	n. s.	p=0.02	p=0.03	n. s.	n. s.	p=0.007
Microtus agrestis	n. s.	n. s.	n. s.	n.s.	n. s.	-	-	-
Totally for small mammal community*	n. s.	n. s.	n. s.	p=0.005	n. s.	n. s.	p<0.001	p=0.004

* all eleven species included.

Whitney pairwise comparison has revealed two pairs of years (of six pairs possible) showing significant differences for single small mammal species (common shrew, yellow-necked mouse, bank vole) and three pairs – for the small mammal community. In the forest the respective results were as follows: two pairs for single small mammal species (yellow-necked mouse, bank vole), and four pairs of years for the small mammal community from six pairs possible.

Community structure

Small mammal community structure in the forest was different from that on the beaver lodges (Figure 3). The most pronounced differences were found in summer (Yates' χ^2 test: $df = 4$, $p < 0.001$), autumn (Yates' χ^2-test: $df = 4$, $p = 0.001$) and in winter (Yates' χ^2-test: -$df = 4$, $p = 0.004$).The proportion of subdominant species, the yellow-necked mouse, was greater in the forest than on the beaver lodges in autumn. On the other hand, small mammal community on the beaver lodges was more contributed by the common shrew than in the forest in all seasons, especially in winter. One more peculiarity of community structure in the forest, share of other species, was nearly zero, whereas on beaver lodges other species taken together have contributed significantly, especially in summer and autumn.

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: $df = 12$, $p < 0.07$). In the forest, the core of the community was formed by dominant bank vole and subdominant yellow-necked mouse. Slight changes in community structure were observed in winter, when contribution of the third species, the common shrew, grew up obviously in comparison with other seasons.

On the beaver lodges, the core of the community was formed predominantly by three species (bank vole, common shrew and yellow-necked mouse). Share of other species was also more significant on beaver lodges than in the forest. In summer, contribution of the short-tailed vole (*Microtus agrestis*) was even greater than that of the yellow-necked mouse on beaver lodges. Moreover, subdominant species on beaver lodges has changed to the common shrew instead of the yellow-necked mouse in the forest. In winter, share of the common shrew grew up to nearly that of the bank vole and the yellow-necked mouse was replaced at all from the small mammal community on beaver lodges.

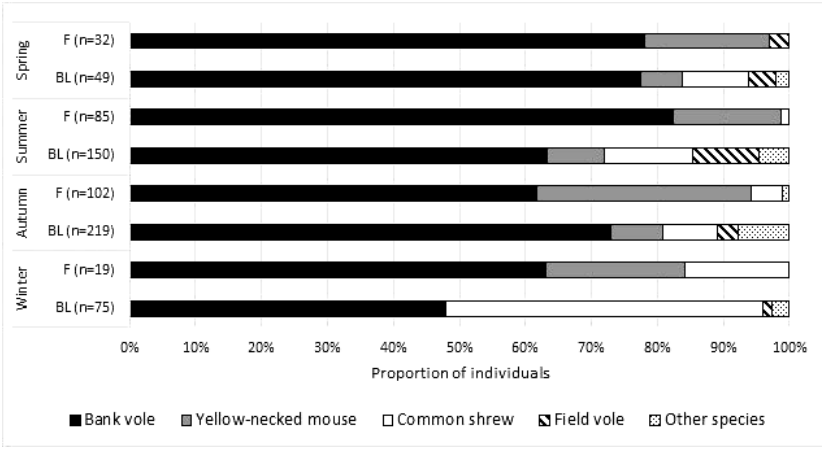

Figure 3. The structure of small mammal community in the forest (F) and on beaver lodges (BL); n indicates the number of captured individuals, n is the number of small mammal

The forest proximity factor

We found that proximity of forest may influence trapping success of small mammals on a beaver lodge. However, among three dominating species this seems to be true only for bank vole in autumn (Table 4). The farther the beaver lodges from the forest were the smaller the TS of bank vole was obtained close to the significance level (Spearman's rank correlation: $p = 0.055$). For other two species this tendency was opposite, but not statistically significant.

Table 4. Spearman rank correlation between the distance of beaver lodges to the nearest forest and the trapping success of small mammals on beaver loges in autumn

Species	*r*	*p*
Sorex araneus	0.1	0.55
Apodemus flavicollis	0.13	0.4
Clethrionomys glareolus	-0.38	0.055

Discussion

Beaver lodges are complex structures made of tree and shrub fragments of different size, mud and turf. Inside the lodge there are beaver-made chambers, holes, ventilation shafts and cavities, which weren't filled with mud accidentally while building a lodge (Ulevičius and Juškaitis 2005). Such a structure could look similar to one that naturally forms in the forest: the root system of the standing tree or dump, microhabitats that occur after the tree falls (Maser et al. 1989). Such cavities and holes both in the forest and in beaver lodges may attract small mammals. It may be used like temporal shelters, feeding, resting, breading and or even overwintering sites (Maser et al. 1989, Merrit 2010).

Beaver lodges may be important for small mammal in winter. Due to specific structure of the lodge the microclimate inside is stable. The mud on the lodge works like a seal and protects the inside from temperature fluctuation (Дежкин 1959, Stephenson 1969, Dyck and McArthur 1993). Because of beaver activities inside the lodge the temperature remains always positive even if the temperature drops below -40 °C outside. The temperature even in abandoned beaver lodges is stable and much milder than outside due to processes of decomposition (Stephenson 1969, Buech et al. 1989, Dyck and McArthur 1993).

Also beaver lodges can be important food storages for herbivores because they are built of different species of trees and shrubs. The fragments of woods vary in size from the big parts of the trunks to the thin branches. Small mammals, like voles and mice, are herbivores, mainly feeding on herbs and seeds in summer (Prūsaitė 1988, Merrit 2010). During observations of beaver lodges in winter season in our study area we have found various signs of small mammal activities. Barking marks on thin branches of *Salix* spp, *Populus tremula*, *Betula* spp, *Padus avium*, *Alnus* spp, *Frangula alnus*, *Quercus robur* were very common (more than 32.4 % of all observed lodges). This indicates that beaver lodges could be attractive not only because of suitable microclimate but also because of higher availability of food. That probably allows small mammals to stay inside the lodge for whole winter.

Beaver lodges cannot be regarded as extensive habitats for small mammals, e.g. like forest. These beaver-built structures due their limited size may serve as important elements of habitat structure at maximum, in which occurrence and abundance of small mammals are rather highly influenced by surrounding habitats (wetlands, forests). However, due high potential for shelter and possibly for food of small mammals, the beaver lodges seem to be important survival stations for small mammals during winter (Ulevičius and Janulaitis 2007), thus, potentially influencing local population dynamics of small mammals in the next reproduction season.

Two species of small mammals caught on beaver lodges, the bank vole and yellow-necked mouse, can be considered as the typical-for-the-forest ones (habitat specialists) (Gurnell1985, Prūsaitė 1988, Mazurkiewicz, 1994, Tattersall et al. 2002). The common shrew, despite its high abundance and occurrence in the forest habitats, can be regarded rather as habitat generalist species (Prūsaitė 1988, Sundell et al. 2012).

Results of our study show the bank vole being the most successful inhabitant of the beaver built structures. Its overall trapping success exceeded as much as four times the trapping success of subdominant common shrew on beaver lodges. Bank vole dominated also in the forest followed by the yellow-necked mouse. The last species seems to benefit from beaver activities only in some cases, especially in warm season, but it was obviously less related with the beaver built structures than the bank vole. The yellow-necked mouse may be less related with the forest in warm season and is able to occupy a variety of habitats in the vicinity of the forest (Prūsaitė 1988).

Possible reasons can be related with some differences in ecological characteristics of these two species. Both species inhabit quite similar forest habitats, however, the yellow-necked mouse is thought to be more related with mature forest habitats (Niethammer 1978, Gurnell 1985), has greater abilities to climb canopy and occupy tree cavities than the bank vole. Also,

the yellow-necked mouse was found tightly related with crop trees in autumn because prefers to feed on highly energetic seeds of oak, hazel, etc. (Juškaitis 2002). Winter food caches by the yellow-necked mouse consisting of these seeds were quite common in nest boxes held for birds and dormice (Juškaitis 2010). The bank vole has far less abilities to climb and basically feeds on small seeds, green parts of plants and bark (Niethammer and Krapp 1982, Prūsaitė 1988). These food categories can be available on beaver lodges throughout the year.

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

Living sympatrically, these two small mammals may compete for resources, which lead to microhabitat partitioning and niche segregation (Hille and Mortelliti, 2010). Under conditions of high densities the physically stronger yellow-necked mouse may force the weaker bank vole from optimal microhabitat (Andrzejewski and Olszewski 1963,Wójcik and Wolk 1985). Our data on trapping success and frequencies of occurrence on beaver lodges indirectly do not confirm the interference competition between 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, in contrast the yellow-necked mouse was more common in the forest in autumn but absent at all on beaver lodges in winter. Moreover, the bank vole showed relatively low inter-annual variation of trapping success on beaver lodges, which indicates stable occupation of this microhabitat in long time retrospective. In our earlier study (Ulevičius and Janulaitis 2007) was registered rather an unusually high number of bank voles on beaver lodges in spring, but only in a single year. Probably it was related with good overwintering conditions or population abundance peak, however in the later years such an extreme trapping success of bank vole on beaver lodges was not observed.

The common shrew showed obvious preference of beaver lodges over the forest in all seasons. This species feed almost exceptionally on matter of animal origin, mainly insects, worms, snails living in the surface layer of soil (Churchfield 1982, Prūsaitė 1988, Hutterer et al. 2008) and prefers cool, damp and shady habitats with dense vegetation, such as riparian forests and reed beds (Neet and Hausser et al. 1990), which is similar to the beaver lodge environments. Common shrews were found at lower abundances than bank voles on beaver lodges. This can be explained rather not by microhabitat selectivity differences between these species, but by different population structure. Common shrews are strongly territorial and their population densities are naturally lower than densities of 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, tending to prefer damp areas (Kryštufek et al. 2008). However, being habitat generalist, at the same time it is defined as a relative feeding specialist requiring highly caloric food. This can cause high intraspecific competition among individuals and may lead to relatively low local densities of short-tailed voles (Myllymäki 1977). 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 in spring.

Small mammals of the rest seven species contributed community structure on beaver lodges but not in the forest. Share of these species grows up in autumn on beaver lodges, probably because of greatest overall abundance of small mammals in this season. Beaver sites itself can be potential habitats for these species. Wetland environments of beaver sites vary in their area size but in some cases can form quite extensive plots of several hectares (Ulevičius 2009).

Generally, our data show that species diversity and community structure of small mammals on beaver lodges can be determined by the surrounding biotopes – mainly by the forest and probably less by other habitats. Individuals of bank vole take about 60-80 % of the forest‘s community of small mammal in Lithuania’s forests (Balčiauskas and Juškaitis 1997, Šinkūnas and Balčiauskas 2005). The similar proportion of bank vole in small mammal community on beaver lodges was found during our studies.

Proximity of the forest was found to enhance trapping success of bank voles on beaver lodges. It looks logically, because the forest habitat is supposed to be the main source of migrants. The yellow-necked mouse and common shrew showed no correlation in this respect, probably because frequency of occurrence of these two mammals on beaver lodges was much lower

than that of the bank vole. Low frequency of occurrence predicts a rather accidental character of habitat occupation and therefore the significant correlations are hardly possible to be found. The yellow-necked mouse was not frequently occurred even in the forest. As it was mentioned before, this small mammal is more strongly related with mature forest or with forest with high seed crops, e.g. hazel stands. In our study area, not all forests were optimal for the yellow-necked mouse, what also could influence the absence of discussed correlation. The eurytopic common shrew (Prūsaitė 1988) may not be related with the forest habitat as strong as the bank vole is.

The trapping success of other small mammals was significantly lower than that of the forest species, even if a beaver lodge was farther from the forest and surrounded by open habitats. This illustrates suitability of the beaver built structures for the three discussed species of small mammals that basically shape small mammal community structure in habitats altered by beavers in the vicinity of forest.

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