

„Impact of Eurasian beaver engineering on diversity, activity and interactions of other mammals”
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Keystone species are considered those organisms, which impact on the other taxa is disproportionately high, compared to their abundance and population density. One of their categories are modifiers, also classified as ecosystem engineers. They provide structures or materials altering habitat, modifying energy flow in the ecosystem and diversity of the other organisms. The exemplary keystone species and ecosystem engineers are North American *Castor canadensis* and European beavers *C. fiber*, which impact results mostly from their foraging on woody plants and damming of streams. Those activities lead to accumulation of deadwood, changes in vegetation structure and wetland creation. The impact of beaver activity includes also the other species of semiaquatic and terrestrial mammals. Despite numerous studies analysing that impact, several gaps in knowledge on that subject persist. Some of its aspects were studied only for North American beaver and/or beaver ponds, while previous research failed to address sufficiently the function of lodges as shelters or foraging sites for co-occurring species. Impact of both beaver species on small rodents and soricomorphs is especially poorly studied, despite their crucial function in terrestrial ecosystems of Holarctic region. Despite the fact, that beaver-altered habitats become centres of activity for the other semiaquatic mammals, knowledge on interactions among them in such sites remains scarce, although that groups include potential competitors, predators and their prey.

The aim of the studies included in the following dissertation was analysing the function of beaver-created structures, i.e. lodges and dams for semiaquatic and terrestrial mammals, as well as impact of that structures on mammalian diversity, abundance and interspecific interactions. They cover three aspects: 1) function of lodges as local centres of mammalian activity and nexuses of their interaction networks, 2) function of dams as dispersal corridors for small and medium-sized mammals, 3) impact of dams and beaver ponds on assemblage of small mammals.

I studied both activity and diversity of mammals visiting beaver lodges in nature reserve „Jeziro Drużno”, northern Poland. Mammalian activity was recorded with trail cameras located on lodges and in control points (surrounding wetland). Except beaver itself, I recorded at least 25 species, including seven invasive species. Share of the latter, especially American mink *Neogale vison* and muskrat *Ondatra zibethicus*, was

significantly higher on lodges. Among native taxa, I found significantly higher frequency of occurrence on lodges for three species, particularly red fox *Vulpes vulpes*, while on controls for three others, particularly red deer *Cervus elaphus*. Species diversity of all recorded mammals did not differ significantly between lodges and controls during the whole year nor in winter, while it was significantly higher on lodges in spring and autumn. On contrary, it was significantly higher on controls in summer. Native species revealed the same, seasonal variation in diversity, as the whole mammal assemblage. I found significant differences in mammal activity between lodges and controls for almost every analysed taxon. For majority of them, both alien and native, the activity appeared higher on lodges. However, that differences were subjected to seasonal variation. The activity of native species co-occurring with beaver was significantly higher on lodges in summer and winter, while the activity of alien species – in spring, autumn and winter. Native mustelids revealed any significant differences only in summer and their activity was higher on controls in that period. Due to predominantly diurnal activity and convergent peaks of activity, temporal niches of American mink and red fox overlapped most strongly among all analysed pairs of taxa. Daily activity rhythms of muskrat and mink mismatched to a significant extent, due to predominance of nightly, crepuscular and dawn activity of the first species. However, activity maxima of the latter predator covered with smaller, diurnal activity peaks of its potential prey, resulting in relatively strong overlap of their temporal niches. Muskrats inhabited almost exclusively lodges that remained uninhabited and only rarely visited by minks. The species that visited lodges, used them for foraging (including scarce hunting), resting, olfactory marking and as vantage points. Five species used lodges as shelters, these were American mink, muskrat, yellow-necked/wood mouse *Apodemus flavicollis/sylvaticus*, bank vole *Clethrionomys glareolus* and Eurasian water shrew *Neomys fodiens*.

To investigate the importance of beaver dams as communication routes for smaller semiaquatic and terrestrial mammals, we used tracking tunnels with kinetic sand as a medium to collect the tracks of animals crossing the three watercourses in Pomerania Lakelands and Baltic Sea Coast. I compared the dams with tree logs connecting the stream banks, while floating rafts were designated as control points. I identified the activity of at least five species of mammals, including three mustelids (stoat *Mustela erminea*, weasel *M. nivalis*, polecat/American mink *M. putorius/N. vison*), one larger rodent (water vole *Arvicola amphibius*), however, most of them were small,

unidentified rodents or soricomorphs, lumped into one category (micromammalia). Logs were more often used by mustelids and dams by rodents and shrews. The highest species diversity was recorded on tree logs, followed by dams and control points. The highest activity was, however, recorded on the dams, when track counts were adjusted for dam width, pointing to the strong selection of that structures by mammals during stream crossing and/or when seeking shelter.

To investigate the effect of beaver damming and flooding on the small mammals' distribution, activity and species richness, I live-trapped terrestrial rodents and soricomorphs in nine wetland sites, located in Pomerania Lakelands and Baltic Sea Coast. Pitfall traps were arranged into transects alongside the watercourses, starting next to a beaver dam. In total, I recorded 12 species: four shrews and eight rodents. The number of captured small mammals and the number of their species were significantly higher on plots subjected to beaver damming. The highest abundance and species richness were found close to a dam and significantly decreased with the distance from a dam. Abundance of five species also declined with that distance, the effect was the most notable for Eurasian water shrew, harvest mouse *Micromys minutus* and yellow-necked mouse *Apodemus flavicollis*. Pygmy shrew *Sorex minutus* demonstrated the greatest degree of dissimilarity in abundance between beaver-flooded and unflooded sections of the transect, clearly selecting the first group. The second most differentiating was *A. flavicollis*, which selected the unflooded plots. Interesting differences were found within the *Neomys* genus, where Mediterranean water shrew *N. milleri* clearly preferred habitats with damming, while Eurasian water shrew was slightly more often caught in habitats without damming, following the already known patterns of competitive displacement observed in Central Europe. Three species (harvest mouse, Mediterranean water shrew, water vole) were trapped solely on beaver-modified plots, while no species was restricted to beaver-free sections of the transects. The observed whole-community facilitation results probably from improved trophic conditions (bottom-up trophic cascade due to nutrient storage in pond sediments), provision of wetland conditions for specialized semiaquatic species and additional shelter (increased herbaceous cover, coarse woody debris, dams).

The studies included in the following dissertation revealed for the first time that beaver lodges act as nexuses of activity and space use by the whole mammal assemblage in lowland riparian habitats, even if their function for some species (mink, muskrat) was already noted in earlier papers. The collected material allowed to reveal

spatio-temporal relations between species forming the assemblage focusing its activity around lodges. I provided also the first evidence for positive reaction of both abundance and species richness of small mammals on damming of streams by beavers, as well as for significant function of beaver dams in maintenance of habitat connectivity for mammals in small river valleys. The additional benefit of my study was testing new medium for tracking pads, which allowed to improve that method of field monitoring of mammal activity.

The collected data confirmed the function of Eurasian beaver as an important tool for maintenance of biological diversity and, therefore, biological conservation, especially during ongoing anthropogenic climate change. It is especially clear in case of small rodents and soricomorphs, as beaver-created wetlands might become significant refugia in human-altered landscape. It is notable that the three species restricted to plots submerged by beaver dams are habitat specialists, already classified as threatened in some European countries. Study on function of lodges for the remaining mammals reveals, however, that opportunities to use Eurasian beaver in biological conservation have significant limits, associated mostly with expansion of alien invasive species, which might be facilitated by beaver constructions. Although native mammalian species are similarly more active and diverse on beaver lodges, it is introduced American mink and muskrat which quantitatively predominate in beaver-associated mammal assemblage. That phenomenon recreates their original interaction with North American beaver from the native range of all three species in the invaded areas of Palearctic. It may partially or completely eliminate potential benefits for remaining, native mustelids or water vole, which that species may obtain from lodge construction by beavers.