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Selection of aquatic vegetation in river habitats by Eurasian beaver (*Castor fiber*) in South-Eastern Norway

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This thesis is worth 60 study points

Abstract

Habitat selection in animals is evident when the choosing of habitat is disproportionate to its availability, usually when habitat characteristics differ in quantity and quality. A very important factor of their use is the availability and suitability of food. Herbivores rely on the vegetation around them for food, and semi-aquatic mammals often use both terrestrial and aquatic vegetation to supply their diet. Aquatic plants are referred to as macrophytes in aquatic botany, and are an integral part of lake and river ecosystems, known to impact both biotic and abiotic features of the environment. Beavers (*Castor* spp.) are opportunistic and choosy generalist herbivores, and will vary their diet with availability and seasonality. Their diet is mainly composed of woody plants such as willows (*Salix* spp.) and aspens (*Populus* spp.) during winter, and grasses, forbs and aquatic plants during summer. Aquatic plants are known to have a higher nutrient content than many terrestrial plants, and beavers forage for example on water lilies (*Nuphar* spp. and *Nymphaea* spp.), water lobelia (*Lobelia dortmanna*), horsetails (*Equisetum* spp.) and pondweeds (*Potamogeton* spp.). We studied aquatic vegetation composition of diving and available locations in river habitats of Eurasian beavers (*Castor fiber*) in south-eastern Norway, to see if beavers selected on certain macrophyte communities over others. We did this in eight beaver territories in the Saua river system in Telemark county. We modelled diving probability with generalized linear mixed models, and found that important diving characteristics included depth, distance to lodge and river edge, sediment type and vegetation cover. Unique insights into diving preferences were obtained, but future research is much needed.

Keywords: Habitat selection, diet, aquatic vegetation, beavers, *Castor fiber*.

Table of contents

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Bø, Norway, May 2020

Marina Eraker Hjønnevåg

Photo taken by me.

1. Introduction

The habitat of an animal will have a set of biotic and abiotic characteristics, matching the requirements of a species to survive. This includes access to shelter and food, and an area to reproduce and disperse (Fretwell and Lucas 1969; Sinclair 2006). The process of choosing a habitat type can be referred to as habitat selection. This is evident when the choosing of habitat is disproportionate to its availability (Johnson 1980; Garshelis 2000). The selection is a result of a patchy environment, where each patch will have resources that differ in quality and quantity, and will together with the presence of competitors and predators affect an animals' use of habitat (Wiens 1976; Hertel et al. 2016). The spatial patchiness can be represented by e.g. varying topography or presence of water. A very important factor is the availability and suitability of food. Usually, animals become more specialized and selective when food is abundant, and more opportunistic when food is scarce (Emlen 1966; Wiens 1976; Rosenzweig 1981).

Models for predicting an animals' diet is based on optimal foraging theory (Belovsky et al. 1989). Ultimately, animals will choose the resources that yield the most energy per unit time (Emlen 1966; MacArthur and Pianka 1966; Emlen 1968; Schoener 1971). The value of a specific food, or prey, is represented by the caloric content divided by search time, capture time and handling time (consumption and digestion) (Emlen 1968; Schoener 1971; Belovsky et al. 1989). Sea otters (*Enhydra lutris*) and river otters (*Lontra canadensis*), for example, need to consume a large amount of prey to suffice their high metabolic rate due to the large cost of diving and swimming (Dekar et al. 2010; Gilkinson et al. 2011). Consequently, river otters' diet will vary with the availability and abundance of crayfish and fish (Dekar et al. 2010). While otters are carnivore and depend on live prey, herbivores rely on the vegetation around them for food.

Herbivores have a large impact on terrestrial and aquatic vegetation, and can alter the species abundance, distribution and the input of different nutrient cycles (Maarel 2005; Maron and Crone 2006). In the Alaskan taiga for example, moose (*Alces alces*) modifies the ecosystem by browsing on deciduous trees in successional ecosystems. By selectively foraging on willows (*Salix* spp.) they alter fine root biomass and mycorrhizal associations, and thereby the soil chemistry. This in turn creates a change from willows to alders (*Alnus* spp.), and in long term a change from deciduous trees to conifers (Kielland et al. 1997; Kielland and Bryant 1998). Moose also forage on aquatic plants as a source of sodium, supplementing their diet throughout the summer (Morris 2002; Tischler et al. 2019). One study found that aquatic plants comprised between 13 % and 27 % of their summer diet (Tischler et al. 2019). Moose forage on e.g. water lilies (*Nuphar* spp. and *Nymphaea* spp.), pondweeds (*Potamogeton* spp.), bur-reeds (*Sparganium* spp.) and quillworts (*Isoetes* spp.) (Fraser et al. 1980; Fraser et al. 1984). Aquatic plants constitute a diverse species group, and have several important ecological functions in addition to being an important food source for many animals.

Aquatic plants are usually referred to as macrophytes in aquatic botany, because they are distinguished from microphytes like most algae, and inhabit areas dominated by water (Gopal 2016). Globally, there are around 2614 species of aquatic plants, and they include vascular and non-vascular plants, such as angiosperms, gymnosperms, pteridophytes and bryophytes, in addition to some macroalgae within divisions Charophyta, Chlorophyta and Rhodophyta. Though, many are yet to be discovered, and wetland species are not included in this number (Lacoul and Freedman 2006; Chambers et al. 2008). Macrophytes are known to be an integral part of lake and river ecosystems, and have a great impact on both biotic and abiotic components. They provide important ecological functions and services, like erosion control, soil formation, hydrological regulation, enhancing water quality, creating habitat and food for many different animals, thus increasing biodiversity, and providing food, fuel and medicine for humans (Gopal 2016).

Macrophytes are usually divided into four categories based on their life form. Most aquatic plants fall into the submerged or emerged group, where both are rooted to the substrate, but grow either wholly underwater or extend above the water surface, respectively. Some plants are however free-floating, either on the surface or suspended in the water. The fourth group consists of plants rooted in the substrate, with leaves floating on the water surface, called floating-leaved plants (Lacoul and Freedman 2006; Chambers et al. 2008; Gopal 2016). These categories comprise a group called hydrophytes, or real water plants. The other group of macrophytes are called helophytes, or swamp plants, and have most of their photosynthesizing parts above water (Mjelde et al. 2000). Many factors impact the abundance and composition of aquatic plants, and this again affects both the aquatic and terrestrial environment and its inhabitants. The most important factors to affect macrophytes include depth and availability of light for photosynthesis (especially for submerged plants), and type of sediment (Lacoul and Freedman 2006; Gopal 2016; Schneider et al. 2018). Other abiotic factors include slope, waves and hydrologic variations. Competition, allelopathy and herbivory are among the biotic factors (Lacoul and Freedman 2006).

Beaver (*Castor* spp.) is another herbivore that feed on aquatic plants. Beavers are opportunistic and choosy generalist herbivores (Vorel et al. 2015) and will vary their diet with availability and seasonality (Svendsen 1980; Bełżecki et al. 2018). Both species of beaver, the North American (*C. canadensis*) and the Eurasian (*C. fiber*), have similar morphology and behaviour (Rosell et al. 2005; Danilov and Fyodorov 2015; Vorel et al. 2015; Alakoski et al. 2019), and are monogamous and highly territorial (Nolet and Rosell 1994). They are important study objects because of their role as ecosystem engineers and keystone species. Through dam and lodge building, they are able to change their environment in a wide range of ways, altercating physiochemical properties and overall structures of their habitat, which in turn will influence both animals and plants within both terrestrial and aquatic communities (Rosell et al. 2005; Pinto et al. 2009).

Beavers are central place foragers, which means that they search for food from a set location, where they also store food and feed offspring. Their central place is their lodge, or on the water (Jenkins 1980; Haarberg and Rosell 2006; Olsson and Bolin 2014). Characteristics describing selected beaver habitat often include areas with narrower river widths, gentler slopes near the river bank (so to give easy access to the shore), shallow waters, low human disturbance, high cover of deciduous trees along the bank, and soft substrates (Macdonald et al. 2000; Pinto et al. 2009). Beavers usually prefer shallow water less than 1 meter deep, and often not deeper than 4 meters (Graf et al. 2018).

The beavers' diet can be divided into three categories; woody plants, grasses and forbs, and aquatic plants. Many studies show a preference towards aspen (*Populus* spp.) and willows when available and dominating an area, but alder, birch (*Betula* spp.), and rowans (*Sorbus* spp.) frequently appear in their diets (Northcott 1971; Fryxell and Doucet 1993; Gallant et al. 2004; Vorel et al. 2015). Woody vegetation is normally eaten during winter when it is stored in a cache near the lodge (Svendsen 1980; Haarberg and Rosell 2006; Milligan and Humphries 2010). Most studies are concentrated on terrestrial vegetation, especially on woody plants. The reason for this, may be the difficulty behind studying aquatic areas, with vegetation being underwater.

In summer, their diet mostly consist of herbs and aquatic plants (Severud et al. 2013). The abundance and nutritional content of aquatic plants decrease in winter due to the cover of ice and snow on the water surface. When they are most available to beavers, in the summer, they have an overall higher content of nutrients like minerals and protein compared to some terrestrial plants. In addition, leaves, stems and tubers are more easily digested, and have less cellulose, lignin and secondary metabolites (Severud et al. 2013). Examples on aquatic plant species foraged on by beaver include water lilies, pondweeds, quillworts, bogbean rhizomes (*Menyanthes trifoliata*), water lobelia (*Lobelia dortmanna*), horsetails (*Equisetum* spp.), bottle sedge (*Carex rostrata)* and common reed

(*Phragmites australis*) (Simonsen 1973; Histøl 1989; Milligan and Humphries 2010; Law et al. 2014a; Law et al. 2014b). Though there are a few studies focusing on water lilies (Law et al. 2014a), and aquatic vegetation is mentioned in some of the older studies on beaver (Simonsen 1973; Histøl 1989), the research on aquatic vegetation in beaver habitat is lacking somewhat. There are for example no studies on aquatic vegetation in the area we are researching.

The aim of this study was to examine the aquatic vegetation composition in river habitats of Eurasian beaver, and study the selection for diving locations. We did this through quantifying aquatic plant species abundance and environmental parameters at diving sites and available sites within territories of Eurasian beavers in south-eastern Norway. We hypothesize here that 1) the beaver population prefers certain plant compositions over others, and 2) that some habitat characteristics are more important drivers for selection of diving.

2.Materials and methods

2.1. Study area

The research was conducted in the Saua river system in Vestfold and Telemark county, southeast Norway, within eight known beaver territories. The river drains Heddalsvatnet in the north and forms part of the catchment of Lake Norsjø in the south. The river area spanned over about 13 km, from Akkerhaugen to the lower parts of Heddalsvatnet. The area measures about 2.5 square kilometres, and is part of the Skien watershed and the Telemark Canal. Its width varies between 45 and 250 meters, with a mean flow rate of <0.6 m/s, which is considered a slow to medium flow rate (Pinto et al. 2009). The area has a cool continental climate (Campbell et al. 2013), with a mean temperature of 6.6°C between January 2010 and December 2019, and a mean annual precipitation of 817 mm ((Norwegian Meteorological Institute 2020). The bedrock consists mainly of feldspathic quartzite and granitic gneisses, with marine and glaciofluvial deposits (Bergstrøm 1981; Dahlgren 2004). The river system is classified as big and clear (< 30 mg Pt/L, TOC 2 - 5 mg/L), low in calcium (1-4 mg/L), low in total phosphorous, ((TP) 4,93 µg/l), thus oligotrophic, and have ecologically good quality related to eutrophication and acidification (Vann-Nett 2020).

The area is comprised mostly of coniferous forest, with Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), in addition to deciduous trees like birch, grey alder (*Alnus incana*), aspen (*Populus tremula*) and mountain ash (*Sorbus aucuparia*). Beavers were almost extirpated in Norway between the mid18th and 19th century, but became a protected species in 1845 (Parker and Rosell 2003). A small population survived in Southeastern Norway, and there have been beavers in Saua river since around 1925 (Olstad 1937). The beaver population has been part of a large ongoing project, carried out by the Norwegian Beaver Project since 1997, which aims to capture and identify all individuals to monitor family group dynamics, and in general their behavioural ecology and movement (Campbell et al. 2012; Mayer et al. 2019). Although there are few predators in the area and the beaver population is currently at carrying capacity (Steyaert et al. 2015).

2.2. Data collection

2.2.1. Beaver capture and GPS logging

From April to June 2019, twelve Eurasian beavers (five females and seven males) from eight territories were captured and tagged (Rosell and Hovde 2001) with GPS loggers (Gipsy 5) and daily diary units (Wildbyte-technologies.com), which included accelerometers and magnetometers. These devices were glued onto the fur on their lower back, and then removed again after two to three weeks. Movements of the beavers were estimated by dead-reckoning, using the acceleration and magnetism data from the daily diary units. Data from the daily diary was calibrated in the software Daily Diary Multiple Tracing (DDMT), developed by Swansea University. The dead-reckoning was done in the software Framework4, also developed by Swansea University (Walker et al. 2015). Dead-reckoning calculates the vector of travel by estimating the magnetic heading, change in positioning and velocity of the animal over time (Bidder et al. 2012). To account for error of the travel vector sequence over time, the movement tracks were ground-truthed using the GPS fixes that were taken approximately every 15 minutes between 7 pm and 7 am (Shepard et al. 2008; Bidder et al. 2015; Wensveen et al. 2015; Dewhirst et al. 2016). GPS positions with horizontal dilution of precision (HDOP) values of > 5 and with < 4 available satellites were removed to correct for imprecision (Lewis et al. 2007).

The movement tracks were divided into 10 second bursts and classified into behaviours based on a behavioural classification model (Graf et al. 2015). The model identifies seven behaviours, clearly differentiated from each other; swimming, diving, sleeping, feeding, standing, walking and grooming. Bursts were classified as dives when the previous 10 seconds were predicted to be swimming. This to filter out potential false dives. Available locations were randomly generated in ArcMap within 95 % minimum convex polygon (MCP) home range covered by water. Both diving locations and available locations were imported into a handheld GPS (Garmin GPSmap 62s) through the program Garmin BaseCamp.

2.2.2. Vegetation sampling

All vegetation sampling was carried out within the study area between medio June and ultimo October 2019 and conducted from a motorboat by two researchers to maintain safety and efficiency. I used a handheld GPS to locate all diving locations for each beaver, in addition to all available sites, as close to 0 meter (m) as possible. When this was impossible, with strong currents and winds, sites were set within 3 m of the GPS location. Locations were excluded when on dry land, and where the river was deeper than 10 m. This was to include vegetation along most of the depth gradient, whilst also taking known depth preferences in beavers into account. All locations were assigned a territory and a plot ID based on the respective beaver and when the dive took place. Depth was registered with a depth measurer, and sediment type using an aqua scope or through film/pictures. Using ArcMap, distance to river edge, territory edge and lodge were measured from each plot.

For vegetation sampling, a quadrat with an aluminium frame of 1x1 m was thrown directly over the zero point of the site. The quadrat construction had a pyramidal shape, so that a GoPro camera (GoPro Hero5) could be attached to the top, 0.8 m above the frame. The height made sure the whole quadrat was within the camera frame when under water. The camera was turned on before being thrown out, and took series of pictures while being held under water. After testing with pictures for a approximately 3 field days in the start, I decided to use films instead, because they were easier to analyse. The frame was left on the bottom for at least 10 seconds when filming, so to let mud settle, and to see vegetation move, which made species easier to identify. Pictures and films were analysed on a computer later. When a plot was shallow, or in swamp areas, the frame was left to film while floristic and environmental data was registered in situ. An aqua scope aided in estimating the vegetation cover and identifying species. Plants were collected with a rake when identification was difficult (e.g. with *Potamogeton* spp.).

The vegetation was determined to be one of four life form categories; emergent, submergent, free floating or floating leaved. I only included macroalgae from the family *Characeae* (order Charales, division Charophyta/Chlorophyta), which is the only group of algae normally included in freshwater macrophytes. Species were identified using Lids Flora (Lid 2005) and Gyldendals store nordiske flora (Mossberg 2012), and name checked through the name data base of Artsdatabanken (Artsdatabanken 2015). Species cover/abundance was estimated by eye, quantified by using a scale from 0 to 100 %, rounding up to nearest 5 percent (Kent 2012). Non-frequent plants with cover less than 10 % were registered with 1 % per individual.

2.3. Statistical analysis

2.3.1. Multivariate analysis of vegetation

I used a detrended correspondence analysis (DCA) to explore my data, consisting of two matrices; the first with species abundances, the second with environmental variables. This was done in R studio (RStudio Team 2019), with R packages vegan (Oksanen et al. 2019) . DCA is a frequently used ordination method to assess similarity and dissimilarity between plots and vegetation composition, that also avoids the arch effect of correspondence analysis (CA), and the assumption of linearity needed for principal component analysis (PCA) (Hill and Gauch 1980; Kent 2012).

The species matrix contained abundances of all taxa from each plot, but only those that occurred more than three times in total were included in the DCA model. This was done to reduce impact of rare species in the analysis. Plots with no vegetation also had to be removed to successfully initiate the 'decorana' function. The data matrix then included 357 observations with 13 variables/species. To see along what gradients the vegetation varied, I fitted standardized environmental variables onto the DCA model. Environmental variables included were depth, sediment, distance to river edge, rock cover, detritus cover, total species cover, species richness and Shannon diversity. Shannon diversity indices were calculated in R for each plot, and the distances to the river edge from each plot were calculated in ArcMap 10.7.1 using the "Proximity" and "Generate near table" tools. The environmental matrix included 357 observations and 8 variables. The variable Sediment was fitted individually to the DCA model because of clutter with the other environmental vectors.

2.3.2. Modelling selection of diving locations within the beaver population

I used resource selection functions with generalized linear mixed effects model (GLMM) to compare diving plots with available plots in the aquatic beaver habitat with a Bernoulli distribution (diving=1, control=0). The data set had a total of 703 observations after removing missing values from modelled variables, in addition to rows with the sediment level 'swamp'. This was due to the lack of these observations in the available plots, and could therefore not be compared to the diving plots. Of the total observations, 236 were diving plots, 467 were available plots. Though the beavers usually moved strictly within their own territory, some beavers wandered into adjacent territories, sometimes into several. In this analysis, available plots where only assigned a beaver if they were within the territory of that beaver. Beavers that belonged to the same territory were assigned the same available plots. All modelling was carried out in R studio (RStudio Team 2019), with R package glmmTMB (Brooks et al. 2017).

Before making candidate models, I checked for collinearity and variance inflation factors (VIF) between all relevant predictor variables. I used a cut-off of >0.6 for collinearity, and >3 for VIF, with functions ‘pairs’ and ‘corvif. I used beaver identification and the territory they belonged in as random effects to account for pseudoreplication, since each beaver were sampled many times within their territory, and to account for variation between territories and traits among individual beavers. Territory was fitted as a crossed random effect. Candidate variables included various species and species classifications, such as life form groups, divisions into graminoids, algae, herbs, angiosperms and pteridophytes. Models with these variables either didn’t converge, or they all had very low explanatory power. These candidate models are therefore not discussed further. Model selection was based on Akaike’s Information Criterion corrected for small sample size and was carried out using the “dredge” function in R package MuMIn (Barton 2019). I selected the most parsimonious model within ΔAICc <2. Confidence intervals for all model variables were inspected to see if they were informative (did not include zero) (Arnold 2010). To validate the top model, I plotted residuals against fitted values for the entire model using QQ plot, in addition to residuals against each predictor variable to look for patterns (Harrison et al. 2018). This was done with R package DHARMa (Hartig 2020).

3. Results

3.1. Aquatic plant distribution and diversity

In total, 580 plots were successfully assessed for vegetation and environmental variables. They were distributed within all predicted territories. The total number of macrophyte taxa found were 30, with 24 identified to species level, and six identified only to genus (*Nitella*, *Potamogeton*, *Sparganium*, *Utricularia*, *Nuphar* and *Callitriche*). Mean species richness per plot was 1.81 ± 1.90, but 6.5 ± 0.5 species per territory, and the highest number of seven species in a single plot. All values stated in the results are mean ± SD, unless stated otherwise.

The most dominant species in the area was water awlwort (*Subularia aquatica*) with a mean abundance of 8.95 % ± 20.10, followed by bulbous rush (*Juncus bulbosus*) with 6.21 % ± 18.59 and intermediate water starwort (*Callitriche hamulata*) with 4.76 % ± 12.48. Intermediate water starwort had the highest frequency (number of plots that the species appeared in) throughout the area, with 27.93 % of the plots, followed by water awlwort with 23.97 % of the plots, and water lobelia (*Lobelia dortmanna*) with 20.86 % of the plots.

Submergent macrophytes dominated the area with a mean abundance of 35.13 % ± 38.19, whereas free floating, emergent and floating leaved life forms had a relatively low occurrence. The only alien invasive species found in the area was Canadian pondweed (*Elodea canadensis*) and it was only found in one territory in lower parts of Heddalsvatnet. Canadian pondweed is in the SE category (severe risk) of the black list (Artsdatabanken 2018). Its mean abundance was 0.46 % ± 5.59. No red listed species were found. See Appendix A for a complete overview of taxa.

Overall, the results of the DCA show a lot of similarity between samples. Most of the plots and species are clustered in the middle (Figure 1), with some scatter to the far left and right. However, DCA axis 1 show a relatively large variation, with an eigenvalue of 0.89 (Table 1). It has a length of 6.31 SD units, which means that there has been a total species turnover between samples to the far left and to the far right. To the left we find quillwort (*Isoetes lacustris*)*;* to the right bottle sedge (*Carex rostrata*), water horsetail (*Equisetum fluviatile*) and small pondweed (*Potamogeton berchtoldii*).

The species in the middle of the biplot are in closer proximity to each other than species mentioned above. Axis 2 has an eigenvalue of 0.61, and a length of 3.63 SD units. Hence, the probability of species along this axis occurring together, is much higher than for the above mentioned. Only stoneworts (*Nitella* spp.) and shoreweed (*Littorella uniflora*), in the top and bottom of the biplot respectively, has a length of almost 4 SD units between them, which makes them less likely to occur in the same plot, at least in the same amounts. There is a half-change between many of the species in the middle, with around 1 SD unit between them, which represent a 50 percent change in vegetation composition of a plot.

Table 1. Eigenvalues and axis lengths from the detrended correspondence analysis (DCA). Eigenvalues show amount of variance along each DCA axis, axis lengths are standard deviation units that represent habitat breadth and beta diversity.

	DCA1	**DCA2**	**DCA3**	**DCA4**
EIGENVALUES	0.8921	0.6062	0.4827	0.3262
AXIS LENGTHS	6.3118	3.6304	3.8080	3.6172

The DCA biplot show relatively distinct groups of species and plots. Group 1 (at approximately -3 SD units on the axis 1, and at 1 on axis 2) contains only quillwort*;* group 2 (within -1 and 1 on axis 1, and -2 and 1.5 on axis 2) contains stoneworts, bur reeds (*Sparganium* spp.), bulbous rush, intermediate water starwort, spring quillwort (*Isoetes echinospora*), alternate water milfoil (*Myriophyllum alterniflorum*), and water awlwort; group 3 (between 2 and 4 on axis 1, and at 1.5 on axis 2) contains small pondweed, bottle sedge and water horsetail. A fourth group forms between -1 and 0 on axis 1, and around -1 on axis 2, with species water lobelia and shoreweed. They are only around 1 SD unit from group 2.

The biplot with fitted environmental vectors (Figure 1) shows that depth explains most of the variation along DCA axis 1 and distinguish between deep and shallow water from left to right. The correlation coefficients for all vectors are found in table 2. Rock and detritus cover vary somewhat with axis 1 and depth, but have a higher correlation with DCA axis 2. The variation along axis 2 is best explained by species richness, diversity and the total vegetation cover, all with scores over -0.89. Rock and detritus cover have higher correlation with axis 2 than with axis 1, but with positive values. Species found in plots with high species richness, diversity and total cover of plants are found in lower parts of the diagram, and the opposite in the top. Overall, richness, diversity and especially total cover decrease with increasing depth, and most species can be found from medium to low depths. Group 1 can be characterized as deep and non-diverse, group 2 as medium deep and non-diverse, group 3 as shallow and non-diverse, and group 4 as medium deep and (relatively) diverse and rich in species.

Table 2. Values of each environmental vector correlated to DCA axes, analysing gradients on macrophyte vegetation.

	DCA1	DCA2	R2	PR(>R)
DEPTH_M	-0.79832	0.60224	0.2311	0.001 ***
ROCKS	-0.58453	0.81137	0.0139	0.146
DETRITUS	-0.68415	0.72934	0.0062	0.422
SPEC_RICH	-0.07592	-0.99711	0.0887	0.001 ***
TOT_COV	0.43659	-0.89966	0.0363	0.011 *
SHAN_DIV	0.25930	-0.96580	0.0863	0.001 ***

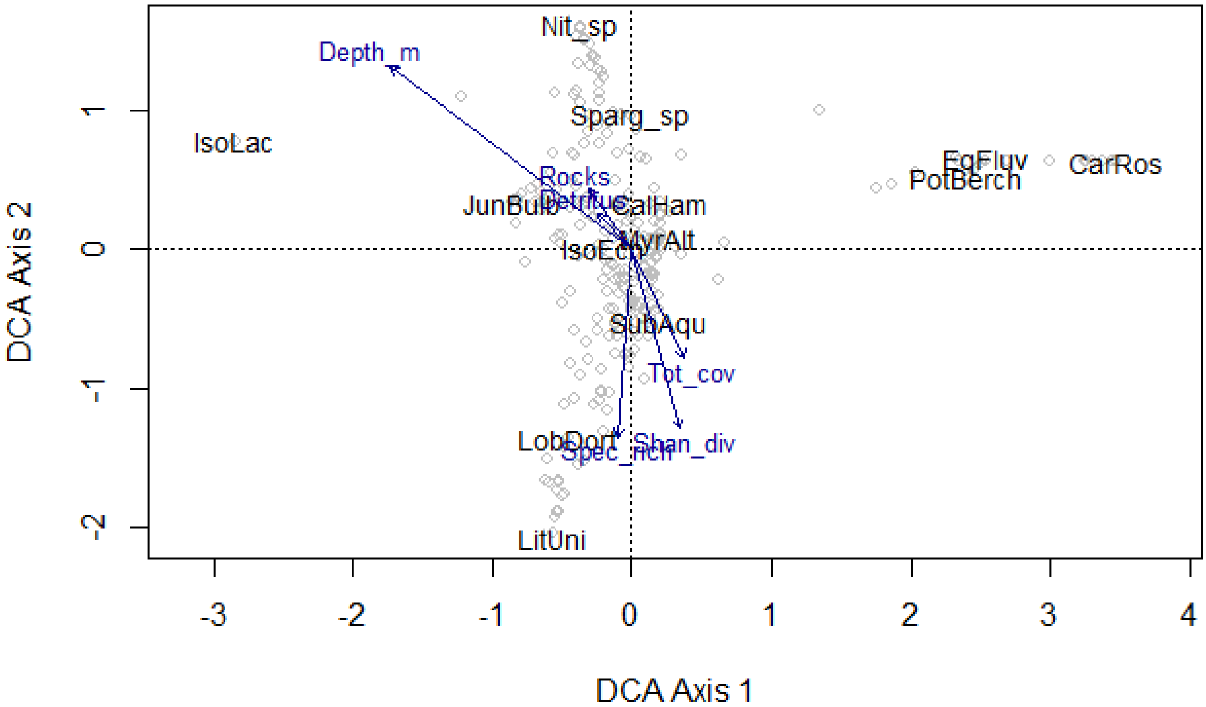

Figure 1. Detrended correspondence analysis (DCA) with species in black text, plots in grey diamonds and fitted environmental parameters with arrows indicating increasing gradients. Depth_m = depth in meters, Rock = rock cover in percent, Detritus = detritus cover in percent, Tot_cov = total vegetation cover in percent, Shan_div = Shannon diversity index, and Spec_rich = species richness measured in number of species. Species abbreviations: IsoLac = *Isoetes lacustris*, Nit_sp = *Nitella* sp., Sparg_sp = *Sparganium* sp., CalHam = *Callitriche hamulata*, JunBulb = *Juncus bulbosus*, MyrAlt = *Myriophyllum alterniflorum*, IsoEch = *Isoetes echinospora*, SubAqu = *Subularia aquatica*, LobDort = *Lobelia dortmanna*, LitUni = *Littorella uniflora*, PotBerch = *Potamogeton berchtoldii*, EqFluv = *Equisetum fluviatile*, and CarRos = *Carex rostrata*.

The sediment types are shown in Figure 2. Bottle sedge, water horsetail and small pondweed appear in areas characterized as swamp. Other sediment types do not really differ that much, and most species seem to occur in many sediment types.

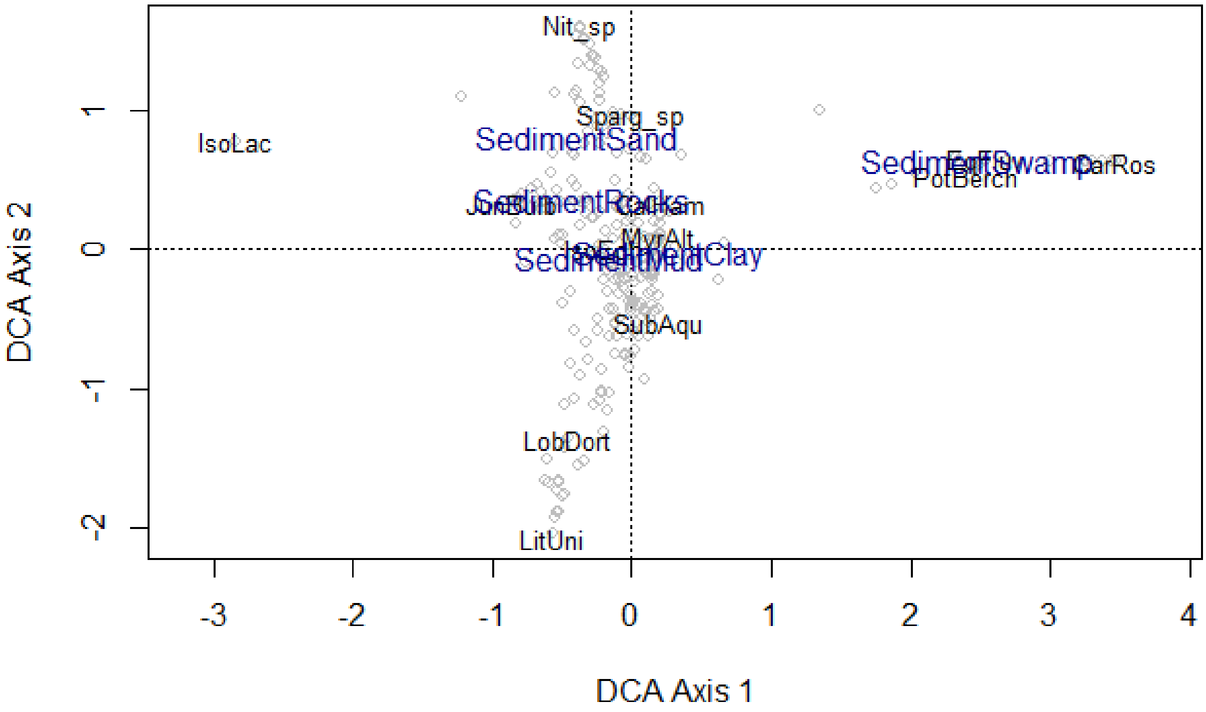

Figure 2. Detrended correspondence analysis (DCA) with species in black text, plots in grey diamonds and fitted environmental parameter Sediment appearing as centroids, with the levels sand, clay, mud, swamp and rocks. Species abbreviations: IsoLac = *Isoetes lacustris*, Nit_sp = *Nitella* sp., Sparg_sp = *Sparganium* sp., CalHam = *Callitriche hamulata*, JunBulb = *Juncus bulbosus*, MyrAlt = *Myriophyllum alterniflorum*, IsoEch = *Isoetes echinospora*, SubAqu = *Subularia aquatica*, LobDort = *Lobelia dortmanna*, LitUni = *Littorella uniflora*, PotBerch = *Potamogeton berchtoldii*, EqFluv = *Equisetum fluviatile*, and CarRos = *Carex rostrata*.

3.2. Aquatic habitat selection in beaver

We retrieved data from nine of twelve beavers, since three daily diary units drowned before being collected. These nine beavers (four females and five males) belonged to five different territories (Table 3). Territory borders of these were defined as the river area covered by 95 % MCP home range of 3188 GPS locations.

Table 3. Distribution of diving plots and available plots in river habitat of Eurasian beavers. Name of beaver, name of their territory, in addition to sex and mean depth per beaver, measured in meter, are provided.

BEAVER	SEX	TERRITORY	DIVES	AVAILABLE	MEAN DEPTH
ANNA	F	Patmos 0 upper	36	76	2.55
CEASAR	M	Patmos 0 upper	26	76	2.90
MASON	M	Patmos 1	19	44	4.15
TATJANA	F	Patmos 1	27	44	3.05
MATANJA	F	Patmos 3	42	41	2.74
LAURITS	M	Patmos 3	12	41	3.17
MAXIMUS	M	Bråfjorden A	4	51	2.16
DYLAN	M	Bråfjorden A	39	51	1.33
TANJA	F	Patmos 4	46	46	1.75

3.2.1. Selection of diving locations within the beaver population

The top model included the explanatory variables depth, total vegetation cover, distance to river edge, distance to lodge, and sediment type (Table 4). For an overview of models with ΔAICc <6, see Appendix B. All variables were informative. The most influential variable upon selection of diving locations was depth (when not counting the levels of Sediment), with an estimate of -0.183. The probability of diving decreases with increasing depth (Figure 4a). Diving plots had a mean depth of 2.44 m ± 2.44, with some beavers more adventurous than others (Figure 3).

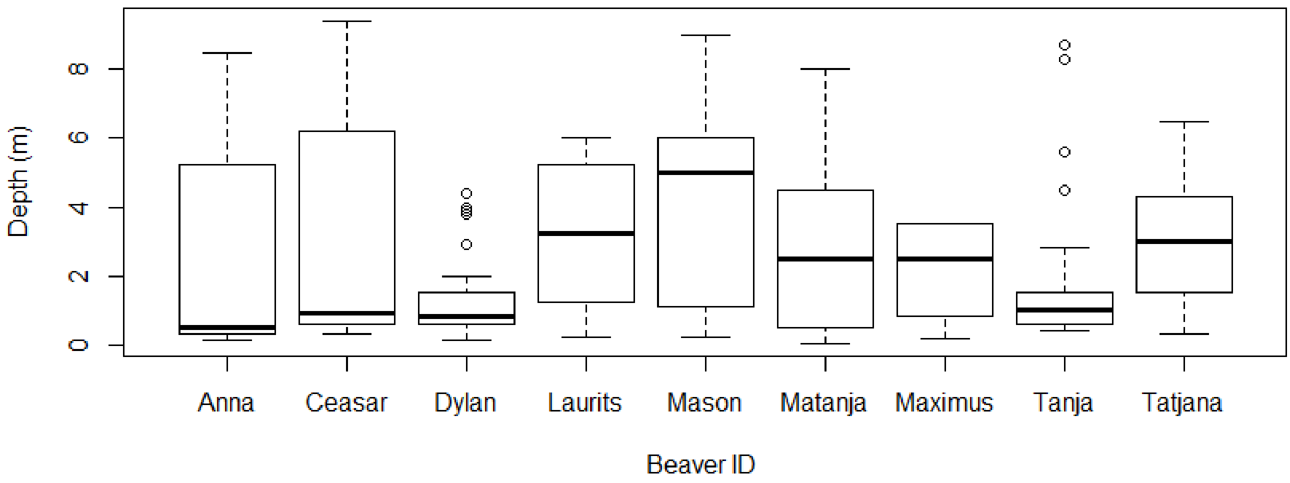

Figure 3. Mean depth of plots where nine Eurasian beavers dived in their river habitat.

The only positive explanatory variable was distance to lodge. Increasing distance to the lodge had a positive effect on the selection of diving sites (Figure 4b). The mean distance to the lodge was 694.34 m ± 667.55. Diving probability clearly decreased with increasing distance to the river edge (Figure 4c), with an estimate of -0.016. The mean distance was 22.09 m ± 27.93. The plot shows that the same happens when the total vegetation cover of the plot increases, though with a slightly less steep curve (Figure 4d). The mean vegetation cover was 32.23 % ± 35.68.

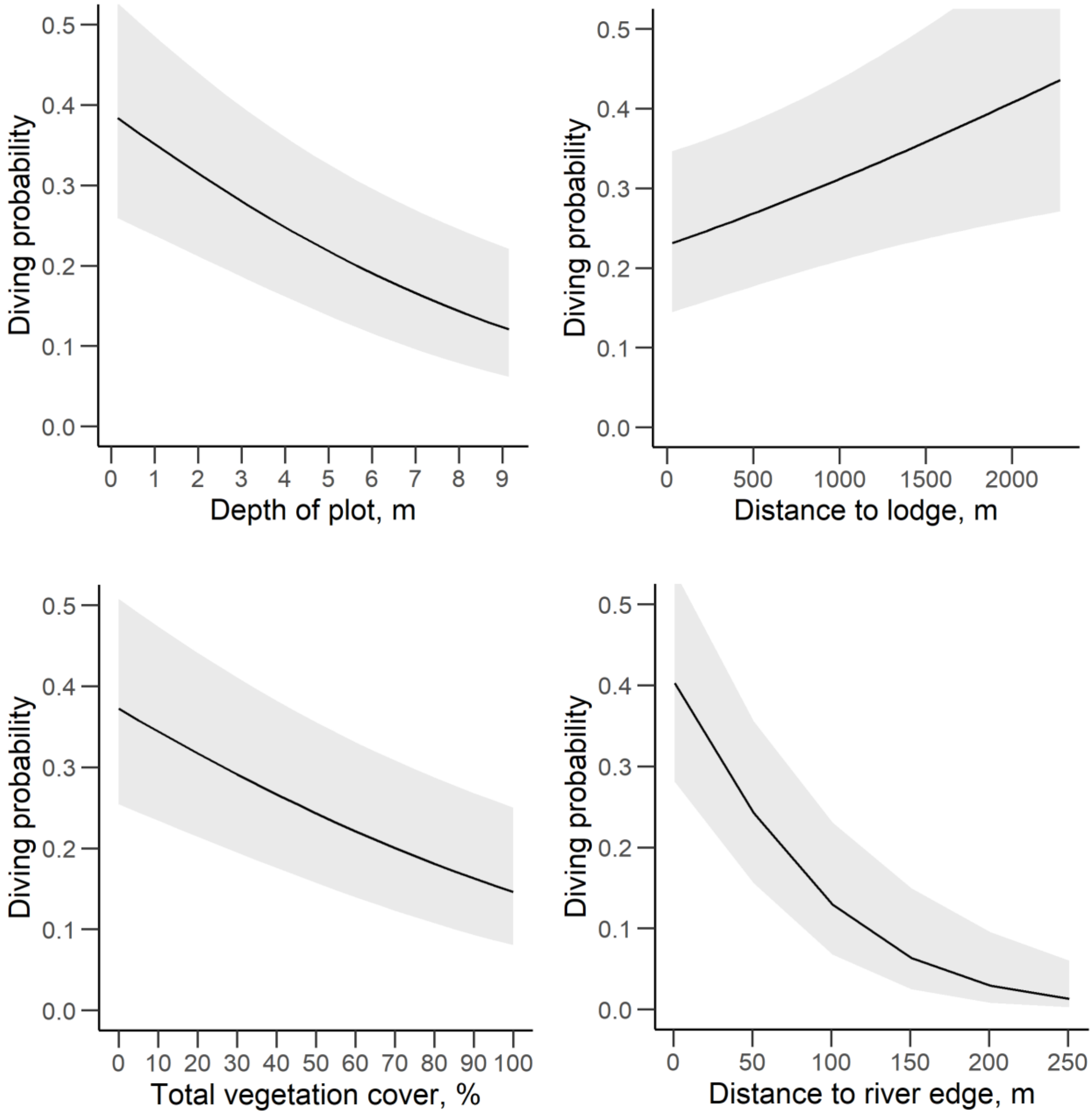

Figure 4a-d. The predicted relationship ± 95% confidence interval between depth (a), distance to lodge (b), total vegetation cover (c), distance to river edge (d) and diving probability in a Eurasian beaver population in south-eastern Norway.

Sediment mud, sand and rocks had a negative effect on the diving probability compared to sediment clay (Table 4). Clay was clearly different from the other sediment types and had a positive effect on diving probability. In addition, mud was clearly different from rocks and sand (Figure 5).

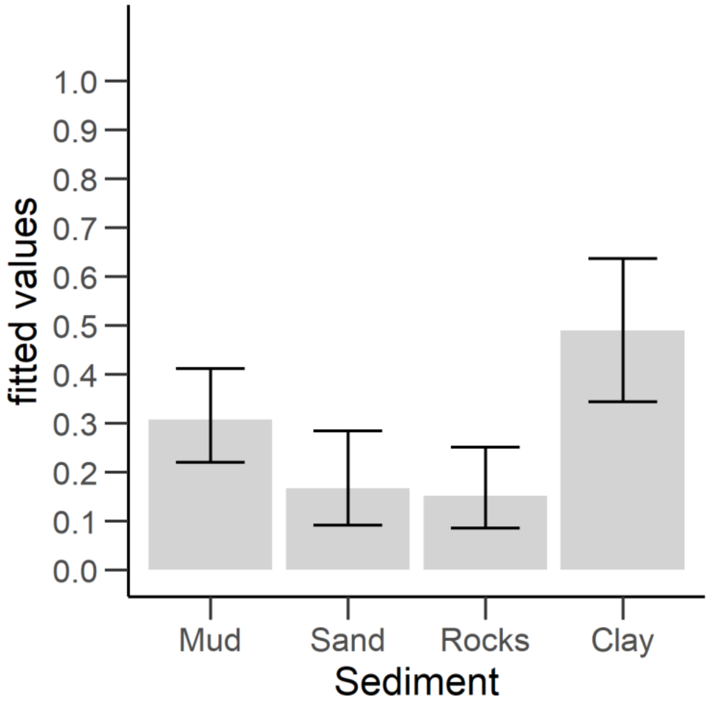

Figure 5. Predicted relationship between sediment types and diving probability in Eurasian beaver population in south-eastern Norway.

Table 4. Model terms from the top model, modelling diving probability in Eurasian beaver population in south-eastern Norway, with estimates, standard error, lower and upper confidence interval. Beaver and territory were used as random effect.

Model terms	**Estimate**	**SE**	**95% CI Lower**	**95% CI Upper**
Intercept	1.326	0.404	0.534	2.117
Depth (m)	-0.183	0.045	-0.270	-0.095
Distance to lodge (m)	0.000	0.000	0.000	0.001
Distance to river edge (m)	-0.016	0.003	-0.023	-0.010
Sediment mud	-0.770	0.278	-1.316	-0.225
Sediment rocks	-1.687	0.355	-2.382	-0.992
Sediment sand	-1.565	0.372	-2.294	-0.836
Total cover (%)	-0.014	0.003	-0.020	-0.007

4. Discussion

The mapping of aquatic plant composition at both diving locations and available locations of beavers have produced important insights into how a semi-aquatic mammal uses its river habitat. When diving, beavers showed a clear preference towards shallow areas near the river edge, but further away from their lodge. Clay sediment and lower cover of macrophytes were important characteristics at selected diving sites.

4.1. Aquatic plant distribution and diversity

The relatively low species richness in the river is consistent with it being clear, oligotrophic and low in calcium. A study in Finland, for example, found between 11 and 31 macrophyte species in clear-water oligotrophic lakes, compared to 50 in meso-eutrophic lakes (Toivonen and Huttunen 1995). There's often a unimodal relationship between number of macrophytes and the trophic level, with little or no vegetation in ultra-oligotrophic, dystrophic and hypereutrophic lakes and rivers, and highest species richness in mesotrophic to eutrophic waters (Lachavanne 1985; Lachavanne et al. 1992; Toivonen and Huttunen 1995; Murphy 2002; Baattrup-Pedersen et al. 2006; Søndergaard et al. 2010; Alahuhta et al. 2017). Most of the species found in our study are also common to oligotrophic lakes and river, such as water lobelia, shoreweed, quillwort, spring quillwort, alternate water milfoil, intermediate water starwort, together with helophytes like water horsetail and bottle rush (Toivonen and Huttunen 1995; Aagaard et al. 2002). Some of the species that occurred however, are more common in mesotrophic to eutrophic lakes, like perfoliate pondweed (*Potamogeton perfoliatus*), common duckweed (*Lemna minor*), yellow waterlily (*Nuphar lutea*) and Canadian pondweed (Aagaard et al. 2002) but were only found in small amounts, usually in shallow water or swamps. Some of the common species found are sensitive to eutrophication of rivers, and work as indicators. Indicators worth to mention because of their relatively high abundance in the area, are bulbous rush, shoreweed, intermediate water starwort, water awlwort, water lobelia and spring quillwort (Penning et al. 2008; Direktoratsgruppen vanndirektivet 2018).

Bulbous rush was one of the most dominating aquatic plants in the area, and is known as a nuisance growth in many European lakes and rivers (Moe et al. 2013; Schneider et al. 2013). When dominating an ecosystem, it makes large stands that results in less suitable habitat for aquatic organisms, thus reducing biodiversity (Moe et al. 2013). It is associated with oligotrophic lakes and rivers that are acidic and very low in nutrients like phosphorus (P) and calcium (Ca) (Schneider et al. 2013).

However, the presence of some long stand macrophytes like alternate water milfoil and pondweed species could indicate that bulbous rush still has other plants to compete with over light and nutrients (Schneider et al. 2013).

The finding of Canadian pondweed is worrying, being reported as the most widespread alien invasive macrophyte in Europe (Hussner 2012), assumed to have mostly vegetative reproduction and also spreading by recreational activities (Anglès d'Auriac et al. 2019). Although it had a very low mean abundance of 0.46 %, and was only found in one territory, the abundance of this species should be monitored regularly to initiate appropriate measures to be able to stop the spread and maintain ecosystem functions and biodiversity.

The depth gradient makes most of the variation in species composition, with quillwort and helophytes at opposite ends of the gradient, and the rest at intermediate depths. Quillwort has its prevalent depth between five and seven meters (Sheldon and Boylen 1977), while bottle sedge and water horsetail are helophytes and exist in shallow water or swamp-like areas (Aagaard et al. 2002). Plants found in the middle of the gradient, e.g. alternate water-milfoil and water lobelia and spring quillwort, are normally present at depths of 1 to 5 meters (Sheldon and Boylen 1977). These results are therefore coherent with the ecology of aquatic plants. With availability of light as a critical limiting factor in water, the decrease in overall cover of vegetation and number of plants is logical. Aquatic plants depend on, among other factors, enough light to do photosynthesis, and the maximum depth of where this can happen is affected by water colour and clarity, turbidity and shading by both riparian vegetation, periphyton and other aquatic plants (Sheldon and Boylen 1977; Lacoul and Freedman 2006).

In future studies, it would be advantageous to measure additional environmental parameters, such as temperature of the water, secchi depth, alkalinity and nutrient levels to examine other important influences on macrophyte communities. This would however be very industrious.

4.2. Aquatic habitat selection in beaver

Although there haven't been much research on diving behaviour in Eurasian beaver, a recent study have found free-living beavers to prefer shallow depths of less than one meter, and no more than four meters (Graf et al. 2018). In another study, beaver presence was associated with areas between one and five meters from the river bank (Pinto et al. 2009). This was believed to be credited shallower depths, though not measured in the study, only indicated by slope angles. This was however not a diving study. Diving preferences displayed by beavers in our study support selection for both shallower depths and areas nearer to the river edge, though we could not establish if the beaver dived all the way down to the substrate, or if they gathered any food there. The diving locations could however indicate where the beaver searched for food, or where it went under to transport materials (Graf et al. 2018). The difference in mean depth at diving locations between beavers might have to do with the differing depths and morphology of each territory, though this was not measured. For later studies, several parameters should be assessed, and a method to identify foraging related to diving should be contemplated.

The preference for dive sites further away from the lodge, there could be several reasons. Beavers tend to build their lodge where the water is deeper, so to get access to the submerged entrance and to build food caches (Dieter and McCabe 1989; Collen and Gibson 2001). This means that there might be lesser species richness and diversity in closer proximity to the lodge, since increasing depth affect this negatively. Additionally, one study suggested that the area around the lodge within a population at its carrying capacity could be depleted of vegetation, and therefore ignored for food (Steyaert et al. 2015). Diving locations near the lodge were not specifically sorted out to be analysed in this study, but would be interesting to research in the future.

Beavers selected clay sediment over mud, sand and rocks at diving locations. Previous studies have shown that beavers prefer riparian areas to be composed of soft substrates such as silt, peat and loam, and that they avoid sediments with sand and rocks (Macdonald et al. 1995; Macdonald et al. 2000; Pinto et al. 2009). This was credited to the more favorable conditions for riparian vegetation growth, and facilitation of burrow and lodge construction. For diving locations, this might be related to the same. Macrophytes usually need to be rooted to the substrate, if not free floating, for anchoring and nutrient access (Lacoul and Freedman 2006). Sand and rocks do not usually fulfill these requirements.

Surprisingly, beavers selected diving locations with lesser macrophyte cover. This might suggest that not all locations were chosen for foraging, or maybe that the precision of the dead-reckoning were too poor. GPSs have an error margin (Schlippe Justicia et al. 2018), and the diving sites could therefore have been located in another area with another vegetation composition and cover. Another reason could be that beavers dived at these locations for something else, for example lodge materials (Graf et al. 2018). If so, it makes sense that they would look in areas where detritus blocked for macrophyte cover. Another reason could be that beavers in truth do not select aquatic plants when foraging. Since predation pressure is low in the area (although present), beavers may prefer terrestrial food over aquatic. Beavers here might forage on aquatic plants somewhat haphazardly, because searching for specific plant species under water is too costly. Beavers are positively buoyant (Fish et al. 2001), and use a good deal of energy on the mechanics and thermoregulatory aspects of diving (Graf et al. 2018). Lastly, there is a discrepancy between when data on beaver movement were collected and when macrophyte abundance is at its peak. The peak is usually in late summer, around August, when the water have had time to warm up (Lacoul and Freedman 2006) Data on beaver movement was registered in April, May and June, while vegetation analysis was conducted between late June and mid October.

5. Conclusions

In summary, we gained important insight into the selection of diving locations within river habitats of Eurasian beavers, with clear preferences within variables depth, distance to their lodge, distance to the river edge, vegetation cover and sediment types. We could not establish any preference towards certain plant compositions in their habitat, and further, more comprehensive research is warranted. Knowledge and an understanding of beaver habitat characteristics and suitability will aid management of the beaver population and their habitat, which could in turn have a big impact on the ecosystem on many levels.

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7. Appendix

Appendix A. Species list from Saua river in south-eastern Norway, with scientific names, common names, mean and SD abundance measured in percent.

SCIENTIFIC NAME	COMMON NAME	MEAN ABUNDANCE (%)	SD
Alisma plantago-aquatica	Water plantain	>0.01	0.04
Callitriche hamulata	Intermediate water starwort	4.76	12.48
Callitriche spp.	Starworts	0.37	4.28
Carex rostrata	Bottle sedge	0.91	8.24
Elodea canadensis	Canadian pondweed	0.46	5.59
Equisetum fluviatile	Water horsetail	1.77	10.70
Equisetum hyemale	Rough horsetail	>0.01	0.08
Isoetes echinospora	Spring quillwort	1.80	7.74
Isoetes lacustris	Quillwort	0.59	6.19
Juncus bulbosus	Bulbous rush	6.21	18.59
Lemna minor	Common duckweed	>0.01	0.12
Littorella uniflora	Shoreweed	2.98	13.09
Lobelia dortmanna	Water lobelia	2.64	7.35
Lysimachia thyrsiflora	Tufted loosestrife	0.02	0.32
Menyanthes trifoliata	Bogbean	>0.01	0.08
Myriophyllum alterniflorum	Alternate water-milfoil	2.03	8.56
Nitella spp.	Stoneworts	4.45	13.72
Nuphar spp.	Water lilies	0.01	0.21
Nuphar lutea	Yellow water lily	0.16	2.66
Potamogeton alpinus	Red pondweed	0.20	4.18
Potamogeton berchtoldii	Small pondweed	0.52	4.84
Potamogeton gramineus	Various-leaved pondweed	1.21	8.47
Potamogeton natans	Broad-leaved pondweed	0.03	0.51
Potamogeton perfoliatus	Perfoliate pondweed	0.05	1.25
Potamogeton spp.	Pondweeds	0.24	2.61
Ranunculus reptans	Creeping spearwort	0.03	0.46
Sparganium angustifolium	Floating bur-reed	0.22	3.22
Sparganium spp.	Bur-reeds	1.24	4.71
Subularia aquatica	Water awlwort	8.95	20.10
Utricularia spp.	Bladderworts	0.12	1.30

Appendix B. Model selection table, with ΔAICc <6. The global model contained the variables Depth_m, Dist_riv_ed, Dist_terr_ed, Dist_lodge, Sediment and Tot_cov, with Use as response variable, and Beaver and Territory as crossed random effects.

	Cnd((Int))	Dsp((Int))	Depth_m	Dist_lodge	Dist_riv_ed	Dist_terr_ed	Sediment	Tot_cov	Df	logLik	AICc	Delta
56	1.326000	+	-0.18270	0.0004648	-0.01648		+	-0.013540	10	-377.689	775.7	0.00
64	1.254000	+	-0.18630	0.0003878	-0.01659	0.0004109	+	-0.013750	11	-376.724	775.8	0.14
62	1.478000	+	-0.19280		-0.01678	0.0006046	+	-0.013560	10	-379.038	778.4	2.70
54	1.662000	+	-0.18950		-0.01659		+	-0.013140	9	-381.457	781.2	5.48

Appendix C. Results of generalized linear mixed modelling, zooming in on sediment. Provided are estimates, standard error (SE), degrees of freedom (DF), lower and upper confidence intervals between each sediment type.

CONTRAST	ESTIMATE	SE	DF	LOWER.CL	UPPER.CL
CLAY - MUD	0.770	0.278	693	0.0533	1.488
CLAY - ROCKS	1.687	0.355	693	0.7743	2.601
CLAY - SAND	1.565	0.372	693	0.6068	2.523
MUD - ROCKS	0.917	0.296	693	0.1549	1.679
MUD - SAND	0.794	0.328	693	-0.0497	1.638
ROCKS - SAND	-0.123	0.388	693	-1.1208	0.876