Roy Duvier

Master thesis

Fantastic beavers (*Castor fiber*) and where to find them Using availability of suitable habitat to estimate beaver populations sizes

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Abstract

The Eurasian beaver was significantly over harvested for its pelt and for what is called castoreum, and the global population was estimated to be 1200 individuals. Today, the Eurasian beaver population is estimated to be approximately 1,5 million individuals spread across a major part of their former distribution range, due to protection of the species internationally and reintroduction programs. The increase in populations leads to a need for a way of estimating population sizes. This thesis' aim is to see if a standardized method can be used to estimate beaver populations accurately. The method uses sign surveys to map suitable habitat, and estimates population size based on the availability of suitable habitat in the study area. I found that the suitable habitat in the area was agricultural- and mixed forest landscapes with waterbody gradients between zero and ten percent slope. The study area has a total of ~18 square kilometer suitable habitat, which leads to a population estimate between 72 – 135 individuals. These estimates seems to be a little high compared to two other methods for population estimation.



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Introduction

The Eurasian beaver (Castor fiber) along with the Eurasian otter (Lutra lutra) are semi-aquatic organisms (Graf et al., 2016), meaning they utilize and live both on land and in water. In addition to the Eurasian beaver there is only one more beaver species, which is native to North America, namely the North American beaver (Castor canadensis). Both species are well known for being so called ecosystem engineers (Wright et al., 2002). An ecosystem engineer is an organism that directly or indirectly dictates the resource availability of other organisms by physically altering the access to or the state of biotic and abiotic factors in the ecosystem (Jones, et al., 1957). Beavers build solid structures of wood, mud/clay, rocks and grasses that function as dams or lodges for the family groups, henceforth called colonies. The beaver is also classified as a keystone species because of its ability to significantly alter the environment in an ecosystem, as well as its ability to create new ecosystems (Collen & Gibson, 2000). It is the effect of dams that mainly leads to the creation of new ecosystems and the altering of habitat. This is caused by the water level increasing and the formation of ponds and small lakes. The consequence of such damming is that the forest and vegetation at the original riverbank will be submerged in water. According to Collen & Gibson (2000) these dams are usually built in streams/rivers and lakes that are not too wide, and in gentle slopes. The beavers, However, might build dams in steeper slopes if the population density is high (Beier & Barrett, 1987).

Another aspect of habitat alteration is the beaver's ability to cut trees. The beavers cut trees in the forest surrounding waterbodies which leads to a more open forest. The felling of trees is a way for the beaver to access the nutrients in the bark. They do not utilize the entire biomass of trees, which makes the remains accessible as food and habitat for other species (Rosell et al., 2005). It's ability to modify both the landscape and the ecosystem makes the beaver an important species where it is native. The habitat alterations, on the other hand, might create socio-economic problems such as damage to landowners' timber when getting flooded. Going back in time however, the beaver was a desired species as it presented a good source of income for its pelt.

The Eurasian beaver was significantly over harvested for its pelt and for what is called castoreum. Castoreum was used for making perfumes but was also used in traditional Asian medicine (Halley & Rosell, 2002). Halley et al. (2012) writes that in the beginning of the 19th century, the total Eurasian beaver population was estimated to be 1200 individuals spread across eight separate areas within their original distribution range. Today, the Eurasian beaver population is estimated to be approximately 1,5 million individuals throughout most of their former distribution area (Halley et al., 2020), due to protection of the species internationally and reintroduction programs. Research has shown that there are potential negative and positive effects connected with reintroduction of the species. The negative effects are usually economical while the positive effects are connected to the ecological aspect. The negative economic effects are usually associated with damage to infrastructure or property (Mikulka et al., 2020), whilst the ecological effects are due to habitat alteration or creation of wetlands (Stringer & Gaywood, 2016).

As previously mentioned, the construction of dams can lead to big, forested areas getting flooded. This might lead to more difficult harvesting of timber, as well as the timber being damaged, causing economical losses for the landowner. Dams can also lead to flooding of roads and blocking of drainage pipes in agricultural fields. If the bank of a waterbody is tall and consists of mud or clay, the beaver might prefer to dig lodges in the bank instead of constructing the characteristic sticklodges, as well as digging tunnels to get up on land (Rosell & Parker, 1995). If such a riverbank borders with an agricultural field these lodges and tunnels might collapse when heavy machinery is being operated in



the field. Such problems implies that there is a need for a good management of the species to reduce economical costs as well as reducing the risk of illegal hunting.

In accordance with Regulation on managing of beavers, the municipalities in Norway recently had to change the way of managing the beaver, as the species juridically was moved from Regulation on management of deer (hjorteviltforskrifta) to Law of biodiversity (naturmangfoldloven). Therefore, quotas and the harvest of beavers no longer is decided based on the length of the waterbody shoreline, but on the population size and if there is a surplus that can be harvested in a sustainable manner. In addition, the beaver is now classified as small game and the municipalities must implement regulations dictating whether there should be harvesting of the population or not (Forskrift om forvaltning av bever, 2017). These regulations should be based on population estimation surveys to map if there is a surplus in the population.

Beavers are both semi-aquatic and nocturnal, and this poses some challenges to the methods used for population estimation. In Norway, population estimation has been conducted in two ways, through a census or an area-based approach, which both has some weaknesses. The census is a reliable and accurate way of estimating the population. It consists of observers walking all the waterbodies in the municipality/area and register all active lodges. The most certain way to determine if a lodge is active or not is based on the presence of a food storage outside the lodge (Hay, K. G., 1958). These storages are made in a short period of time during autumn, between when the temperature starts to drop and the ice settles on the water. Thus, the survey is limited to a short period of time, which will make conducting a census in a big area difficult as it is a highly time-consuming method. As it takes a long time to conduct, it becomes an expensive way of estimating the population size.

The area model on the other hand is based on data collected from census work, where the total area of a municipality is divided with the population estimate from the census. This has shown in most areas to be on average 0.26 beaver colonies per square kilometer. This estimate has been the base for the wildlife management in municipalities in Norway, taking the estimate of 0.26 and multiplying it with their own municipality area, to get an estimate of colonies (Parker et al., 2013). The number of colonies is then multiplied with the number of individuals per colony to get an estimate of the beaver population. This method is highly cost effective and doesn't take more than a minute. This method does not, however, consider the topography of the area, nor how long beavers have been present. For instance, if used by a municipality which is largely covered by high alpine areas but has beavers in the lower parts, the total population size can be overestimated. These estimates have been developed in areas where the beaver has been present for decades, and the population has settled at a level where they start utilizing suboptimal habitat due to population size and competition for resources (Rosell & Campbell-Palmer, 2022). So, if the area model is to be used in an area where the population is only present in the optimal habitat, this method is also likely to result in overestimation.

The aim of this thesis is to find out if a standardized method can be used to map suitable beaver habitat in an area, and to get a more accurate population estimate based on the availability of suitable habitat. A standardized method could be to use a grid-based approach to choose transects for sign survey and using the environmental and beaver sign data to run a suitability analysis. Further, territory and colony sizes from the literature can be used to estimate the population size.

The aim of this thesis has been to answer the following questions:

- Does the grid based transects give a representative sample of the area?
- Are beaver signs a good indicator of suitable habitat?
- What habitat types are preferred in the area?



- How much suitable habitat is available in the area?
- Does the method give an accurate population estimate?



Materials and methods

This study consisted of two separate surveys. The first was a standardized survey according to a protocol described by Duvier (Duvier, 2020) in which an observer performs a sign survey based on transect locations. In these transects the observer records all signs from beaver activity, as well as environmental factors surrounding the transect. The second survey was performed as a census where active beaver lodges were counted within the same area as the standardized survey. Both surveys were performed in the period 23 to 29 November 2021. Late autumn is a good period for surveying beavers because this is when the beavers build up their food storages (Busher et al., 2020). The fieldwork was carried out by five observers including myself.

Study area

The study area was the south-western part of Midt-Telemark municipality, Vestfold and Telemark County, more specifically south of the Bø river in the former Bø municipality (Figure 1). Bø is an area with scattered human settlements and a more densely populated city center. Most of the study area consists of forests and agricultural landscapes.

Bø was chosen as the study area as the beavers have been present there since the 1920's (Pinto et al., 2009), resulting in a stable population distributed in both optimal and sub-optimal habitats (Rosell & Campbell-Palmer, 2022; Rosell & Parker, 2012). In addition, the Norwegian Beaver Project at University of South East Norway has been conducting extensive research on beavers in the area for decades, including a census of the population in 1997. In addition to having historical data, the head of the project assisted with organizing fieldwork and input on the method.

Study area

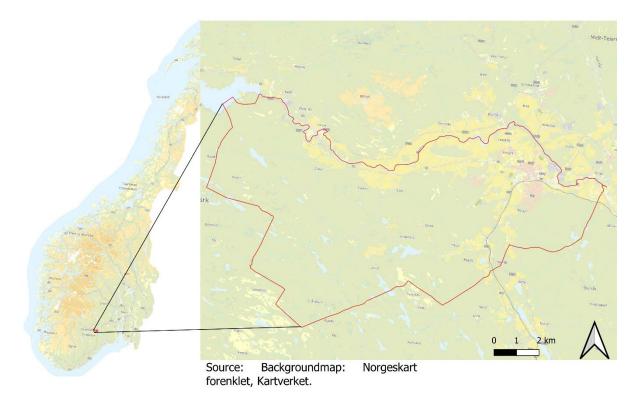


Figure 1. Location of the study area in Norway, with a more detailed inset map outlining the study area in red.



The standardized method I used in this study is based on creating a grid to distribute transect points evenly throughout the study area. I created a grid of 1.3x1.3 km using QGiS version 3.18.3 with GRASS 7.8.5 (QGIS, 2022), where each crossing point in the grid marks one transect and added it to a background map of the study area. As beavers are semi-aquatic and are dependent on water, the transect points that did not overlap with water, were moved towards east until they overlapped with a waterbody. The final transects are marked with points, and results in a skewed grid of 58 points. The coordinates of the transect points were then downloaded and added to a GPS application for smartphones (Norgeskart outdoors). Each points marks the middle of a 1 kilometer transect that was surveyed, meaning the observer had to survey 500 meters of the riverbank/lakeside in each direction from the point.

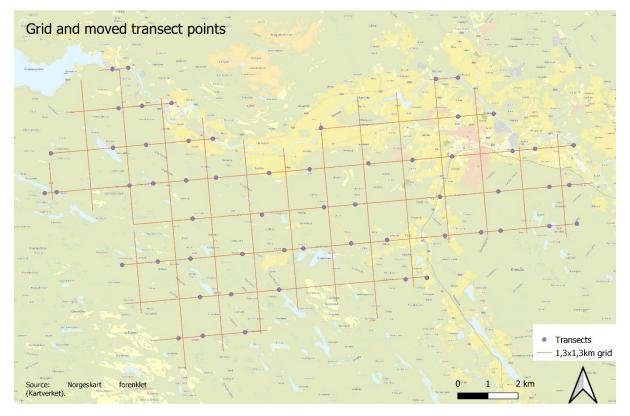


Figure 2. Grid and location of transects after being moved towards east.

Fieldwork

Standardized method

In the standardized method we surveyed all but three locations from the points created by the previously mentioned grid. The observers used smartphones with the GPS app Norgeskart Outdoors to find their way to the transect points and to make sure they walked the entirety of the 1 kilometer transects. During each transect survey the observer registered which forest type was the most dominant through the transect (coniferous, deciduous, or mixed), type of waterbody in which rivers and streams were classified as running water, and lakes and ponds were classified as still water. Furthermore, the observers registered if the transect ran through wetlands/bogs, the amount of gnaw marks (categorized as old, from this year, and fresh), number of beaver dams, number of beaver



lodges, number of trenches, and presence of food storages at the lodges. I decided to register gnaw marks on trees, trenches, dams, lodges, and food storages, as they are the most certain indications of beavers being present in an area (Hay, 1958). If the transect was within 20 meters from roads, houses, or other human construction it was classified as an urban environment. Transects passing through (within 20 meters) agricultural landscapes were classified as agriculture.

The observers also noted down a small description of the surroundings of each transect, such as if the forest was dense or open, if there were clearcuts along the transect, if the stream was rocky or steep, and other factors that might influence beaver presence along the transect. The sign survey was conducted by 5 observers 4 of which have a background in ecology, and one which has local knowledge and has an interest in beavers. Different observers can lead to some potential errors in the classification of the environment of the transect, age of signs and detectability of signs, lodges, and food storages. All the observers got an introduction in how to classify the age of signs and shown pictures of all the types of signs to be registered including lodges and food storages. At the end of every field day the observers met to discuss findings, especially those they were uncertain of while in the field. All observers were instructed to take photos of the lodges found, as well as dams and food storages to validate field-classification in the evening meetings.

Another possible difference between the observers could be the ability to detect all signs along the waterway, and each observers view on what is a coniferous-, deciduous-, or mixed forest. This possible source of error was tried to be mitigated by creating a protocol for how to classify the environment. The environment description was based on a 20-meter zone from the shoreline along the transect. Another source of error for the environmental aspects of the survey, was the potential mismatch between each individual's definition of forest type compared to the definition used in the geodata acquired from the Norwegian Mapping Authority. This can potentially lead either under-, or overestimation of the amount of suitable habitat in the area.

Census

The census was performed by walking or canoeing the full length of waterbodies and registering coordinates of every beaver lodge found, taking notes if they were active having a food storage outside or inactive if they did not. In addition, information about what type of waterbody (running or still water), type of area (agriculture, bog and/or forest type), and human presence (human structures) were registered.

I aimed to conduct a census in the study area as a way of validating the accuracy of the suitabilitybased approach to population estimation. However, after completing the full stretch of Bø river I realized that I could not complete a census of the entire area due to lacking funding and time, after performing the standardized method survey. Unfortunately, this resulted in the standardized method standing without a highly accurate validation regarding population estimates. Given this, I have used the area method as a pointer to see how much it varies, in addition to comparing my population estimates with the census from 1997 (Rosell & Parker, 1997). I chose to use the 1997 census as an indicator of accuracy as beaver populations after being present in an area for over 40 years are quite stable in terms of population size (Rosell & Parker, 2012), given there has been no drastic population reduction due to hunting or stochastic events.



Beaver tracks and signs

Gnaw marks

Gnaw marks include standing trees with gnaw marks on the trunk, as well as felled trees and debarked branches. As previously mentioned, the gnaw marks were categorized into 3 age categories: fresh, within one year, and older than one year.

The gnaws are categorized by appearance and color; fresh gnaws are tree white/light yellow, and for Salix spp. the twigs will be light green if they are fresh, as remains from the inner layer of the bark is still attached to the wood. Gnaws from within one year are typically white and look a bit dry and can also start to become light grey in color. The gnaws that are older than one year tends to be completely grey/dark grey, have some moss growth (very old), or have a thick layer of sap in the cut and appear yellow/orange.

Trenches

What is called trenches in this paper is paths the beavers frequently use in and out of the water, tunnels they've dug in the riverbank to get on land, or channels they've dug inland to increase food access and escape routes in case of predators. The dug channels are easily recognizable, the trenches from exiting and entering the water, however, can be mixed up with frequently used paths from other wildlife crossing the river. So, to decide if it is a beaver trench or not, a trick is to use a stick to touch the river/lake bottom. If it's from beavers! will feel quite hard due to the repeated use of the trench.

The trenches were categorized as either active or inactive based on the presence of fresh gnaws next to it.

Dams

Beavers build dams in shallow and somewhat narrow streams and rivers to increase the water level and make it more stable through the year. This makes it possible to build burrows or lodges with an entrance under the water. Therefore, dams are a good indicator of beavers being present in an area, however the dams are solid constructions and will remain in the environment long after the beavers in the area are no longer present. I categorized dams as intact or broken, based on visible leaks or breaks in the dam, in addition I looked for new logs on the dam.

Lodges

Beavers build lodges of sticks and mud, dig burrows if the riverbank/shoreline is suitable and high enough for digging, or a mix between the two. The lodges/burrows both has their entrance under water to prevent unwelcome guests from entering. The characteristic stick lodges blend well with its' surroundings and can be hard to spot, especially if there are no new logs been added to it recently. The burrows are almost impossible to detect unless the water level is so low that the entrance is exposed, or if there is a food cache in the water. Lodges were classified as active or inactive purely based on the presence of food caches (Hay, 1958).

Food cache

Beavers in areas where the water freezes over during winter create a food storage to survive, as the ice prevents them from going on food search on land. The food caches consist of sticks that the beavers cut in the late autumn/early winter as the temperature starts to drop. They press the sticks/branches into the riverbed/lakebed to ensure they stay under the ice. When you come across food caches they appear as a pile of branches in the water a little off the shore and are usually easier to spot than the lodge right next to it.



Data processing

Microsoft Excel

I used a Microsoft Excel (2018) spreadsheet to organize all notes from the fieldwork in a table to make it ready to be used in RStudio, and to make some simple plots to illustrate the data.

RStudio

I used RStudio version 4.0.2 (Rstudio team 2022) with packages dplyr (Wickham et al., 2022) and ggplot2 (Wickham, 2016) to analyze the data and select which variables to use in QGIS. To do this I ran 3 binomial generalized models using all recorded beaver activity as the response variable. The first model included all the environment and slopes as explanatory variables, in the second model I excluded slopes as a variable and removed two rows containing the activity observations in deciduous forest and in marshes. These were removed since they were the only two locations with deciduous forest and marsh, respectively. The last model only contained slopes as an explanatory variable.

QGIS

I used QGiS version 3.18.3 with GRASS 7.8.5 (QGIS, 2022) to run a suitability analysis. I chose QGiS as it is a free software that is user friendly and has many tools to process geographical data at the same level as other purchasable GiS programs. The suitability analysis in QGiS is based on raster data, so firstly I made sure all my geodata, such as waterways, land area cover, and slope were all raster data. To make the suitability analysis consider the variation in the beavers foraging distance inland I created a proximity raster containing 4 different distance classes, 0-50, 51 - 100, 101 - 200, and more than 200 meters (Rosell & Campbell-Palmer, 2022).

Beavers tend not to settle in fast flowing rivers and streams due to the difficulty of building dams and lodges. The literature describes the upper limit of slopes at 15% for beaver occupancy (Curtis et al., 2004; Rosell & Campbell-Palmer, 2022). Therefore, I reclassified the slope layer into 4 classes, 0-4%, 5-9%, 10-15%, and more than 20%.

Further I extracted the different habitat types from the environment raster into separate raster files and reclassified the value of cells according to the results from the model in Rstudio.

Lastly to create a raster file containing the suitability analysis, I used the raster calculator function. The raster calculator is a command module that requires codes/commands, and to get the desired layer according to the model, I used this code "("freshwater_reclass100@1")*("under 20 slopes test2@1" + "Mixed_reclass@1" + "Agriculture_reclass@1" + "Open terrestrial area@1" + "Human structures transport@1" "Deciduous_reclass@1" "Coniferous forest@1" and + + + "Bog@1")*"raster_boundary@1"". Where freshwater_reclass100@1 is the freshwater layer containing different foraging distance classes multiplied by 100 to make the visual representation in the map clearer. The freshwater layer is then multiplied by all the other habitat types and area covers. Further this code is multiplied with the raster extent of the study area to restrict the layers to the respective extent. I then changed the symbology of the raster file to give me 4 classes, not suitable, less suitable, suitable, and very suitable. Further I exported the area covered by all 4 classes to an excel file.

Processing of suitable habitat data

The dataset exported from QGiS is in square meters for the different suitability classes. And as working with square meters is unnecessary, I converted it to square kilometers. With the square kilometers of suitable habitat, I calculated the number of territories this area can support, however beaver territories, unlike other species', are described in linear distance (kilometers) and not square



kilometers. A study in Bø "Territory and group sizes in Eurasian beavers (Castor fiber): echoes of settlement and reproduction?" (1998-2000) found the average territory size to be 4 kilometers, with a lowest size of 1.9 and largest size of 6.1 km (Campbell et al., 2005). I converted these linear territories into square kilometers by multiplying them with their foraging range inland which are described to be from 0- 20 meters from the water, and up to a maximum of 200 meters. I divided this foraging area into 3 categories to create a minimum, average, and maximum foraging area. This creates 9 estimates from minimum territory size multiplied by minimum foraging range to maximum territory size multiplied with maximum foraging range.

Having the territory sizes in square kilometers I divided the total of less suitable, suitable, and very suitable habitat by the square size of each of the nine estimated territory sizes. This results in how many territories the suitable habitat can hold. Further I multiplied the number of territories with minimum (2.4), average (3.8), and maximum (4.5) colony size (Rosell & Pedersen, 1999) to get population estimates for the study area.



Results

Standardized method

I found beaver activity at 32 out of 53 (60%) survey locations (figure 3). The transects with activity were distributed across the study area, except for a drier forest area in the center and the more urbanized areas toward the east.

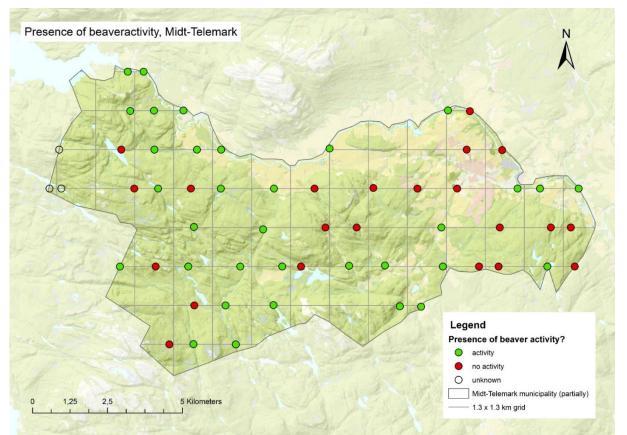


Figure 3. Green dots indicate beaver activity along the transect, red dots indicate no activity, and black circles is transects not survey. Map made by Wessel Veenbrink.

Figure 4 shows that mixed forest was the environment with most transects (N = 33), of which 22 contained beaver activity. Agricultural landscape was the second most frequent environment (N = 13) of which 9 contained activity. Coniferous forest was found in 5 transects, whereas only one had any activity. Bog, urban and deciduous was only found in one transect each, where the transects in bog and deciduous forest both contained activity. The transect in urban landscape did not contain any activity.

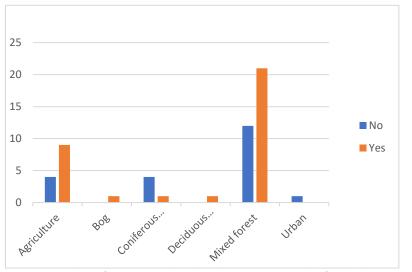


Figure 4. Number of transects with and without activity in each of the habitat variables.



As illustrated in figure 5, most transects were found to be along waterbodies with a gradient steeper than 20% (N = 21), in which 11 of the transects did not contain any beaver activity. Waterbodies with a gradient less than five percent were the second most recorded, in which 15 contained beaver activity (N = 17). Gradient class 5-9% had 3 transects with activity out of a total of 8 transects. There was 5 transects in gradient class 10-15% where 4 contained beaver activity.

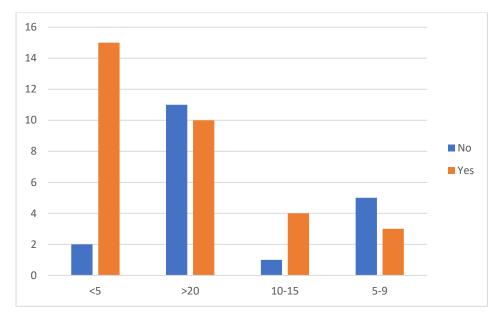


Figure 5. number of transects containing activity/no activity in each gradient class.



Model estimates

I found that within the study area the probability of finding active beaver lodges (N = 13) was highest in mixed forests (probability: 0,67%, P > 0.05), followed by agricultural landscapes (probability: 0.08%, P = 0.01) (figure 6).

I also found that it is more likely to find active beaver lodges in lower stream gradients 0-4% (probability: 0.6%, P = 0.03), followed by 5-9% (probability: 0.46%), and a 0.12% probability in stream gradients steeper than 20%, which both have a P > 0.05 for both (figure 7).

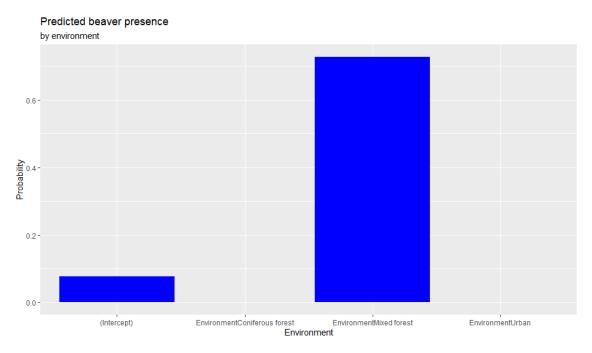


Figure 6. Probability of presence of beaver lodges in different habitats. Intercept is agricultural landscape.

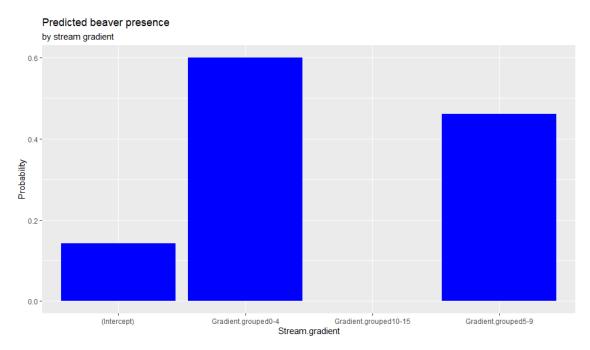


Figure 7. Probability of presence of beaver lodges in different stream gradients (in %). Intercept is >20%.



Regarding beaver presence in form of any visible activity (figure 8), I found a higher tendency (P > 0.05) to observe activity in agricultural landscapes (0.69% probability), followed by mixed forest (probability: 0.42%), and lastly in coniferous forest (probability: 0.1%).

Further, figure 9 shows that the probability of observing signs was highest for streams with gradient between 0 and 4 % (probability: 0.8%, P = 0.013), closely followed by streams with gradient between 10-15% (probability: 0.80%, P = >0.05), then streams steeper than 20% (probability: 0.48%, P > 0.05), and lastly streams between 5-9% (probability: 0.38%, P > 0.05).

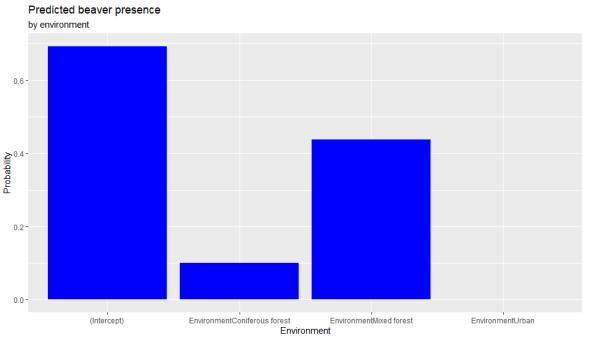


Figure 8. Probability of presence of beaver signs in different habitats. Intercept is agricultural landscapes.

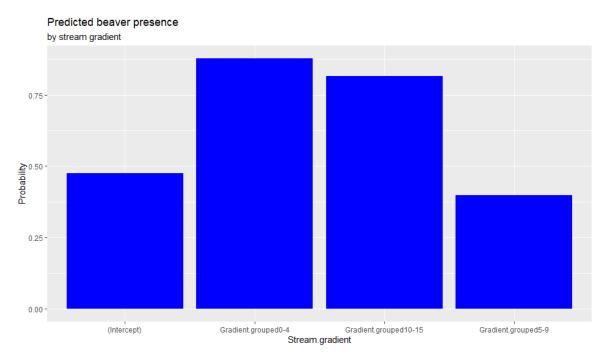


Figure 9. Probability of presence of beaver signs in different stream gradients (in %). Intercept is >20%.



Suitable habitat

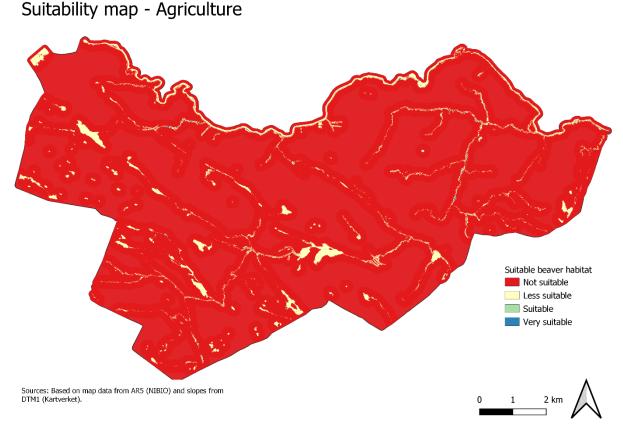


Figure 10. Suitability map of the study area where agricultural landscape was ranked highest in the suitability analysis.

Figure 10 shows the study area covered by suitable habitat when agricultural landscape was weighted highest in the analysis. Most of the area is not suitable for beavers (18.37 suitable habitat out of 104 total square kilometers), mainly due to being at longer distance than 200 meters from waterbodies and coniferous forest being the dominant area cover in the study area. The category "very suitable" only accounts for approximately 0.5% of the total suitable habitat, whereas the category "suitable" habitat was 30%, and less suitable 69.5%.

Territory sizes

Territory sizes Territory size 50m Territory size 100m Territory size (km) (km2) 200m (km2) (km2) 6.1 0.305 0.61 1.22 Max Average 4 0.2 0.4 0.8 1.9 0.095 0.19 0.38 Min

Table 1. Converted territory sizes from river stretch (km) to river stretch multiplied by forage area along the riverbank (50m, 100m and 200m).

Converting the linear territory sizes into area by multiplying with the three different foraging distances gave 9 territory estimates (table 1). With a minimum territory size of 0.095 and a maximum of 1.22 square kilometers.



Territories

Table 2. Number of territories the less suitable, suitable, and very suitable area can contain.

Number of territories	Territories (50)	Territories (100)	Territories (200)
Min	60.21	30.11	15.05
Average	91.83	45.91	22.96
Max	193.32	96.66	48.33

The total suitable habitat in the study area (figure 1) is estimated to hold between 15 and 193 territories (table 2), when dividing the total suitable area with the territory size estimates from table 1.

Populations Estimates – standardized method

Tables 3-5 show the minimum, average, and maximum number of territories (pulled from table 2) multiplied by minimum, average, and maximum colony size to give population estimates based on the agriculture landscape suitability analysis. The population estimates for the area varied greatly from a minimum 36 individuals to a maximum of 870.

Table 3. Calculated from territory size 50.

Number of territories	Min colony size	Average colony size	Max colony size
Min	145	229	271
Average	220	349	413
Max	464	735	870

Table 4. Calculated from territory size 100.

Number of territories	Min colony size	Average colony size	Max colony size
Min	72	114	135
Average	110	174	207
Max	232	367	435

Table 5. Calculated from territory size 200.

Number of territories	Min colony size	Average colony size	Max colony size
Min	36	57	68
Average	55	87	103
Max	116	184	217



Census

I found beaver lodges in 18 of 53 survey transects, of which 7 were active (having a food storage). In the census of the upper stretch of Bø river there was a total of 11 lodges, of which 6 had food storages (figure 11). Resulting in a total of 13 active and 29 inactive lodges observed in the whole study area.

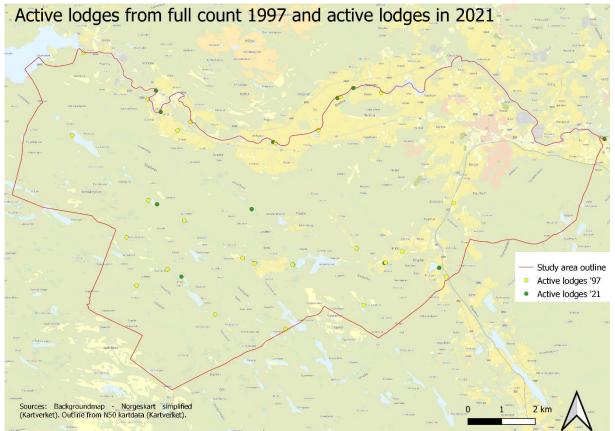


Figure 11. Map of active lodges (lodges with food cache) found during fieldwork 2021 (green), and active lodges found during a full count in 1997 (source: unpublished data, Frank Rosell & Howard Parker).

Population estimates - census and area model

The beaver population in the study area was estimated to be 65 (min), 103 (avg), 122 (max), using the area model and the simple formula; N = 104 (total area) * 0.26 (colonies per km2) * colony size. Using the census data from 1997, the population would be estimated to be 60 (min), 95 (avg), or 113 (max) using the following formula: N = 26 (active lodges) * colony size.



Discussion

The standardized method is, as mentioned, based on the use of a skewed grid to select locations for the sign surveys. The benefit of using this approach is that transects are evenly distributed in the area and prevent bias in placing transects where there is known to be beavers. It does, however, not cover all waterbodies in the area like in a census. This means there is a possibility that the transects from the grid does not cover enough of the area to give a representative sample of the habitat in the area. For instance, if the grid is too wide, it is a chance that habitat types that are less common in the area will not be sampled, which could lead to a bias in the dataset. Using a smaller sized grid gives a better resolution and a better sample of the area, the grid will then reflect the abundance of the different habitat types instead of missing them. I only had one location that was classified as deciduous forest in this survey, which is a good reflection of the area cover of forest types in Bø, which is mainly dominated by mixed and coniferous forest. Given the range of habitats in my survey, it seems the grid based transect gives a representative sample of the area.

Beaver signs are easy to spot and recognize, and a certain indicator of beavers being in an area, past or present. Beaver signs are therefore the most used method to estimate the species' distribution in an area. It is, however, lodges/burrows with food storage that is described as the only certain indicator of an active colony occupying an area (Hay, 1958). For instance, a beaver dispersing to an unoccupied area might pass through habitat that is not suitable and forage on the way, thus leaving signs. This creates an uncertainty in whether these types of signs are a good indicator of beaver habitat preferences. This uncertainty can be mitigated by age classification of the signs as well as the number of signs present in the transect. A dispersing beaver will not produce a big number of signs until it has found the area it will occupy, hence a large number of fresh signs is a good indicator of beaver utilizing the habitat. Beavers also alternate territories, they can deplete their food resource in their territory, but then move to another one while the first one recovers (Rosell & Campbell-Palmer, 2022) . Thus, I argue that also a substantial number of older signs are an indication of suitable habitat as the area must have been suitable, and most likely will recover and be occupied again.

Looking at the prediction plots, the highest probability to find beaver activity is in agricultural landscapes followed by mixed forest (figure 8), these two habitats are switched if looking at active lodges (figure 6). Both response variables do, however, result with the same two habitats, and one possible reason for agriculture scoring higher when looking at all activity, can be that it is typically easier to spot signs in an open agricultural landscape compared to a denser vegetated forest. Another possibility mixed forests score higher in the prediction model based on active lodges, is that in agricultural landscape the shoreline is typically taller and consists of mud and clay. This shoreline composition is suitable for the beavers to dig burrows instead of building lodges (Rosell & Campbell-Palmer, 2022), which reduces the detectability.

When it comes to the suitability of a habitat based on the steepness of the waterbody, the model with lodges as response variable showed a clearer trend towards the lower gradients, while the model with all activity as the response predicted beaver presence quite high for all the classes. This might be because lodges will only be built where the likelihood for the lodge or dam to be destroyed by floods are lower, such as, where the stream is gradient is low (Rosell & Campbell-Palmer, 2022). The signs from beavers in higher gradients can be, as previously mentioned, due to dispersing to new areas, or from foraging. The stream gradient doesn't affect foraging as much as it affects the construction of lodges and burrows, as they are capable of swimming in a stronger current and can move on land and avoid moving in the water in rapids (Beier & Barrett, 1987). Thus, it seems that all signs of activity can be used as an indicator of habitat suitability. Thus, I argue that using signs from all activity, not just



active lodges, is a good way of mapping the full range of habitat features the beaver utilizes, and not just where it is suitable to build lodges. Based on the prediction models, waterbodies with a low gradient between 0-10% in agricultural- and mixed forest landscapes are suitable habitat in the area.

As mentioned, the beaver has been present in Bø since the 1920's (Pinto et al., 2009), and since beaver populations reach their carrying capacity after 40-50 years (Rosell & Parker, 2012), the population should now be stable. The literature often describes deciduous forest as the strongest predictor for beaver presence, however, this might be a result of most beaver habitat surveys being conducted in relation to reintroduction programs or initial population in a new area (Pinto et al., 2009), where the beavers only occupy optimal habitat (Rosell & Campbell-Palmer, 2022). Beavers are a generalist herbivore, and as the population increases and the optimal habitat is occupied, they start inhabiting sub-optimal habitats (Rosell & Campbell-Palmer, 2022). This is well reflected in my models where agricultural- and mixed forest landscapes show the highest probability of beaver presence.

When combining the stream gradient, environment preference, and the foraging range in the suitability analysis, it estimates that 17.6% of the study area is suitable beaver habitat, when all suitability classes are pooled together. This is quite a high percentage, given that the suitable habitat is limited to 200 meters from the shorelines. It is, however, the category "less suitable" that makes up most of the total (12.80 km²), followed by suitable (5.47 km²), and very suitable (0.09 km²). This shows how important it is to not only map the most optimal habitat, but also the sub-optimal habitat the species utilizes. On the other hand, it is unlikely that beavers frequently utilize the entire 200-meter buffer, as beavers prefer to stay as close to water as possible (Donkor & Fryxell, 1999; Haarberg & Rosell, 2006; Rosell & Campbell-Palmer, 2022). This mismatch might lead to an overestimation of the suitable habitat in the area.

The standardized method has a big variance in estimates for population size from 36 to 870 individuals. This is a result of a snowball effect from of having three territory size estimates, along with three different foraging distances, and three colony size estimates. It does seem that using the minimum number of territories calculated from the 100-meter foraging distance gives the best population estimates, when compared to the area model and the census from 1997. The minimum, average, and maximum estimates from the standardized method lies roughly 10 individuals above the respective categories from the area model, and about 20 above for the census. Based on these comparisons it seems that my method overestimates the population slightly. I argue that this is due to the snowball effect, but also the potential overestimation of available suitable habitat. These two factors need to be refined in order to make the standardized method yield accurate population estimates.

The standardized method has potential to influence management of the species in Norway and other areas in the species' northern range. It also has a potential as an accurate and cost-effective population estimation method. Using this method to map suitable habitat based on sign surveys creates a small index of suitable habitat in the area. Habitat suitability indices (HSI) exist for several wildlife species, and are used to predict their distribution in an area (Zajac et al., 2015). There is such an index for the North American beaver made in Canada and The US (Anderson & Bonner, 2014). As the two species differ in preferred habitat and effects on the landscape (Müller-Schwarze, 2011), creating a different HSI for the Eurasian beaver is necessary. The standardized method has since 2019, been conducted in 10 different study areas as part of bachelor theses at the Inland Norway University. Pooling these datasets will give a solid HSI for the species in Norway, and potentially making the sign surveys obsolete.



To achieve the aim of developing a standardized method that is accurate and cost-effective, I suggest further research is carried out. One of the issues that needs to be investigated is which foraging distance to use for the barrier of suitable habitat, as well as finding a way to implement better territory size estimates. The latter is a bit difficult as beavers, In contrast with other territorial wildlife species, don't seem adjust their territory size according to the optimality of the area they occupy (Campbell et al., 2005). Campbell et al., 2005 further describes that instead; the size of the territory is decided by how dispersing pairs enter unoccupied areas. Meaning if multiple pairs enter the area at the same time, the territories will be smaller, whereas if they enter at different time, the first pair will likely claim a bigger territory. Furthermore, it would improve the accuracy of the standardized method to map suitable habitat at vegetation level as beavers don't only forage on trees. Beavers, especially during summer, also forage on other vegetation, such as, herbs, roots and agricultural crops (Rosell & Campbell-Palmer, 2022). This is, for now, difficult to implement in Norway as vegetation datasets are limited.



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