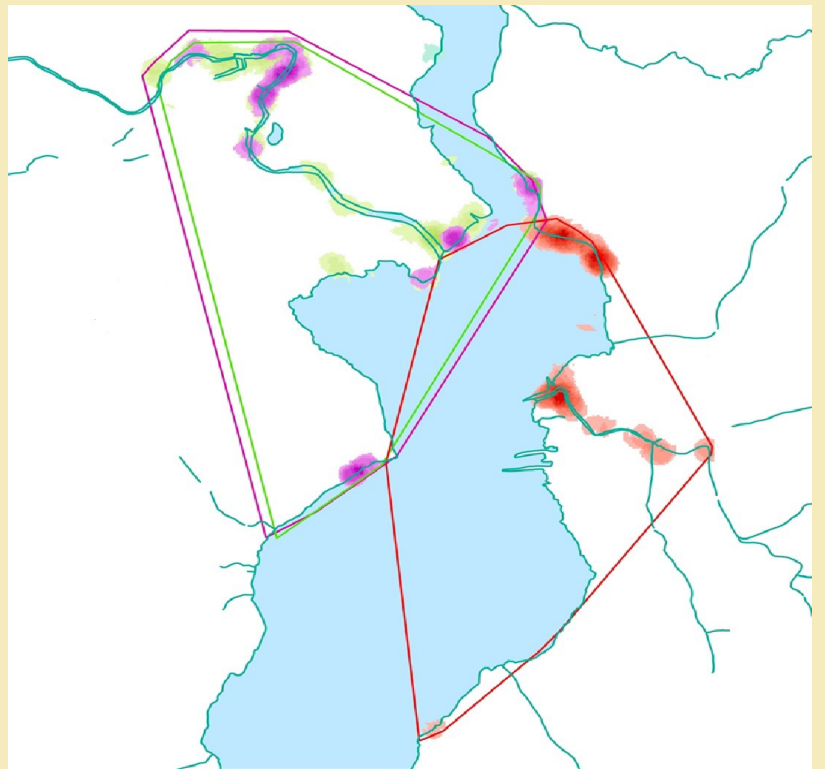


Master Thesis

Manuel Echeverria

“GPS-aided mapping of  
Eurasian beaver (*Castor fiber*)  
territories in southern Norway”



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## GPS-aided mapping of Eurasian beaver (*Castor fiber*) territories in southern Norway

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### Abstract

In this study I use GPS technology for the first time on the monogamous semi-aquatic Eurasian beaver (*Castor fiber*). I tested the hypothesis that GPS technology can be used in the riparian environment. Further I tested the hypothesis that beavers do not show sexual behavioural dimorphism by measuring territory size, distance travelled and activity patterns. I also predict that overlapping of territories will be located at the borders. I attached GPS tags on 18 dominant individuals ( $\bar{x} \pm SD$  weights) males ( $23.0 \pm 1.1$  kg) and females ( $24.0 \pm 2.3$  kg), and 4 subordinates (males =  $15.2 \pm 1.7$ ; females =  $18.7 \pm 5.3$ ) in Telemark county, southern Norway. GPS tags were deployed for  $12.7 \pm 4.3$  (7 – 24) days with a sampling rate of 15 minutes from 19:00 to 7:00 resulting in  $443 \pm 41.1$  (190 – 811) locations per animal, during the months of April to October from 2009 to 2011. I calculated territory sizes by measuring 95% and 50% cores by using two different Home range estimators; the Minimum Convex Polygons (MCPs) and Kernel Density Estimator (KDE). Further with the resulting polygon from the MCPs I calculated territory sizes as river bank length. The measurements for the 95% cores showed no significant differences between the estimators. The 50% cores measurements showed significant differences indicating greater accuracy for the KDE. My results suggest that beavers do not show sexual behavioural dimorphism in activity, territory size and distance travelled. Territory overlap between neighbours resulted in  $7.4\% \pm 7.4\%$  (0.05 – 31.2%) for KDE measurements and  $15.5\% \pm 15.1\%$  (0.03 – 43.2%) for MCPs, overlap occurred only at the 95% cores corroborating the hypothesis. Mated pairs (N = 3) overlap resulted for MCPs  $88.4 \pm 11.1\%$  and KDE  $84.1 \pm 5.3\%$  showing that they shared the same territories, supporting the hypothesis that Eurasian beavers are a strictly monogamous species. GPS technology allowed beaver territories to be defined with high precision, providing a better understanding of the spatial behaviour and activity of beavers and greatly reducing tracking efforts and costs.

**Keywords:** activity, behaviour, *Castor fiber*, GPS, nightly distance travelled, territory

## Introduction

Knowing an animal's movement and space requirements is a key factor in understanding species behaviour and their ability to persist in time (Thomas et al. 2004). Given the increasing pressure humans have on natural habitats, understanding how animals use their habitat is of major relevance in wildlife management and conservation policies (Schofield et al. 2007). Collection of behavioural data from some nocturnal species by direct observation is difficult due to a substantial proportion of daily activity occurring between dusk and dawn or out of sight of the observer (Hulbert et al. 1996, McConnell et al. 1999).

Using technology for animal tracking started in the early 1960's, relying on Very High Frequency (VHF) technology (White and Garrot 1990). VHF transmitters are attached to the chosen individuals and tracked by researchers using receivers from land, air or water. The drawback of this technique is that in order to triangulate animal positions receivers need to be close enough to the animals, and the accuracy achieved varied from  $\pm 70 - 600$  m (Recio et al. 2011). Therefore researchers need to be in the field, with the potential problem of affecting animal behaviour and with high demand of manpower and time (Cooke et al. 2004).

The first GPS units utilised in wildlife research were of a considerable size and studies were limited to large mammals with enough body dimensions to hold the weight of the GPS and its batteries, such as wolves (*Canis lupus*) (Merril et al. 1998), moose (*Alces alces*) (Rodgers et al. 1996) and African elephants (*Loxodonta Africana*) (Douglas-Hamilton 1998). However, now that devices are smaller and lighter, it is possible to target a wider array of smaller species such as feral or domestic cats (*Felix catus*) (Recio et al. 2010), brushtail possums (*Trichosurus vulpecula*) (Dennis et al. 2010) and hedgehogs (*Erinaceous europaeus*) (Recio et al. 2011). Recent advances in GPS technology has allowed studies to be performed in marine environments on sea turtles (Schofield et al. 2007). Quaglietta et al. (2012) tested GPS GSM/GPRS devices on wild otters (*Lutra lutra*) with positive results in a freshwater riparian habitat. This evolution in GPS technology presents a unique opportunity to further test its performance in the riparian habitat. Studies in semi-aquatic mammals that live in this habitat present many major challenges such as: canopy enclosure (Hulbert and French 2001, Frair et al. 2010), lodges or burrows that animals visit, preventing the GPS from having a clear sight of the sky for several hours a day (Blakie 2010) and submersion since this can affect proper GPS functioning (Quaglietta et al. 2012).

The Eurasian beaver (*Castor fiber*) is a suitable model species in which to test GPS functioning and accuracy in the riparian habitat. Beavers are Eurasia's biggest rodent and are generalist herbivores that live along fresh water bodies; they are semi-aquatic mammals of

nocturnal habits that live in lodges or borrows (Sharpe and Rosell 2003). They are central place foragers with a core area, usually around the main lodge, where they return often during active periods (Wilsson 1971). They feed on shoots, leaves, tree bark and water plants (Haarberg and Rosell 2006). Their role in freshwater ecosystems and their ability to modify the environment to their own benefit has earned them the name of ecosystem engineers; they cause modifications on streams and water levels through damming, thus helping the regeneration of the riparian habitat through the removal of trees (Fustec et al. 2001, Rosell et al. 2006). They concentrate their feeding at the water's edge in order to reduce energy expenditure and mortality risks, with some foraging under the forest cover and away from the water (Pinto et al. 2009, Campbell et al. 2012). A typical beaver colony is composed of an adult monogamous mating pair, kits of the year, yearlings and occasionally one or more sub-ordinates; this last class can be mature animals that due to a lack of territory availability are forced to remain in the colony (Campbell et al. 2005).

Beavers are one of the few mammals that display strict monogamy, creating mating bonds that span for many years (Rosell and Thomsen 2006). Both dominant individuals share territorial protection and rearing the young. They have only one territory that is shared by all colony members and is maintained throughout the year by means of aggression and scent marking by all colony members > five months in order to secure resources (Wilsson 1971). Beaver territories are defined areas where neighbouring territories overlap only at the borders, and territory overlapping between sexes is exclusive to their mate or other colony members (Herr and Rosell 2004, Campbell et al. 2012). This territorial behaviour could be the result of plants needing several years to regenerate, so ensuring exclusive access to resources guarantees long term survival (Fustec et al. 2001) and prevents resource depletion (Nolet and Rosell 1994). Beavers present little anatomical dimorphism, with females reaching body sizes equal to those of males (Rosell and Thomsen 2006). Their activity is also similar with both animals being out of the lodges at dusk for feeding and patrolling, seasonal variances arise due to parturition with most females giving birth during the first 3 weeks of May (Parker and Rosell 2001, Sharpe and Rosell 2003), and both sexes returning often to the lodge during the night (Wilsson 1971).

Traditional VHF tracking has been successfully used on beaver studies in the past, but it proved to be time consuming and on occasion inaccurate (Nolet and Rosell 1994, Herr and Rosell 2004). I propose that GPS tags can positively aid in animal behaviour studies; reducing drastically tracking time in the field and can be effectively used in mapping territories and to obtain enough data to derive answers about border dynamics on population at carrying capacity (Pinto et al. 2009). In this study I use GPS tracking for the first time on the Eurasian beavers. I

test the hypothesis that beavers do not present behavioural sexual dimorphism, by measuring three basic behavioural aspects; territory size, distance travelled by night and activity patterns. I predicted that overlap with neighbouring territories will be located at the territory borders and with no overlapping at the 50% cores. I also compare the suitability of using two of the most widely used home range estimators, Minimum Convex Polygons (MCP) and Kernel Density Estimator (KDE) (Nilsen et al. 2008, Laver and Kelley 2008) for determining territory sizes in the Eurasian beaver.

## **Materials and methods**

### ***Study area***

This study was carried out between spring 2009 and spring 2012 in a population of free-ranging beavers in the rivers Straumen (59°29′ N, 09°153′ E), Gvarv (59°386′ N, 09°179′ E), and Sauar (59°444′ N, 09°307′ E) in Telemark County, southern Norway (Figure 1). The climate is cold and wet with a mean annual temperature of 4.6 °C and an annual precipitation of 790 mm (Campbell et al. 2012). All rivers flow through a semi-agricultural landscape interspersed with riparian forest. The proportion of forested area on the river sections studied varies between 40.5% and 52%; this woodland is dominated by grey alder (*Alnus incana*) and, to a lesser extent, willow (*Salix* sp.) and bird cherry (*Prunus padus*), with some dry deciduous and coniferous forest (Haarberg and Rosell 2006, Pinto et al. 2009). The Sauar and Gvarv rivers are regulated along part of their length with weirs and locks, ensuing only moderate variations in water temperature and reduced ice cover in winter (Campbell et al. 2012). The Straumen River forms part of the Telemark Canal and the section used in this study was bound at each end by canal locks and weirs. The entire study area has human settlements and scattered houses, and all rivers are used for leisure activities with frequent boat traffic. Beavers in the study area do not build dams, presumably since all rivers are large enough to make damming unnecessary (Herr and Rosell 2004). Beavers have been in the area since the 1920s (Olstad 1937) and face little or no hunting pressure (Parker et al. 2002, Campbell 2005).

### ***Study animals***

The beavers in the study area have been monitored between March and November every year since 1998 through an extensive live-trapping program allowing beavers to be identified by their ear-tags/microchip (Campbell et al. 2012). We captured the animals at night from a boat with a landing net, and transferred them head first into a cloth sac where they were immobilised and easier to process. Measurements of body and tail length, and weight were taken for each

individual (Rosell and Hovde 2001). This method is simple, does not require for the animals to be anaesthetised and it has been approved by the Norwegian Directorate for Nature Management and the Norwegian Experimental Animal Board.

We targeted known dominant individuals, but in some territories where we were unable to trap the dominant animals, and thus we trapped non-dispersing sub-ordinates. Sex and status within the colony statuses were determined by previous trapping and sighting records.

### ***Tagging***

We equipped beavers with a VHF transmitter (Reptile glue-on, series R1910; Advanced Telemetry Systems) with a weight of 10g, along with a rechargeable archival  $\mu$ GPS receiver (Figure 2a) (model G1G 134A; Sirtrack, Havelock North, NZ, <http://www.sirtrack.com>), weighing 24g. GPS and VHF units were glued onto the fur of the lower back of the animals, using a two-component epoxy resin (Figure 2b), because that part of the body is higher when swimming thus allowing better sight of the sky. A coarse meshed polyester fishing net was used to cover the units and reduce likelihood of removal by the animal. GPS tags were deployed with a sampling rate of once every 15 minutes from 19:00 to 7:00 according to beaver's nocturnal habits (Sharpe and Rosell 2003). Average handling time ranged from 30 to 40 minutes depending on air temperature and the solidification time of the resin. For retrieval, animals were re-trapped with the same procedure and the transmitters were cut out of the fur with a scalpel. Handling time on retrieval varied between 15 to 40 minutes; depending on how close to the skin the resin had solidified.

### ***Data preparation***

Prior to analysis, the raw data was screened for location errors using the values of Horizontal Dilution of Position (HDOP). HDOP is an estimation of the likely horizontal precision of the location as determined by the satellite geometry (Sirtrack GPS Receivers Manual, Sirtrack, Havelock North, NZ). I chose HDOP = 4 as being personally recommended by the manufacturer as the highest acceptable value with minimum error in the dataset given that accuracy degrades with higher HDOP values. I also removed the locations obtained by the GPS that were on the days of capture and retrieval to avoid biased behaviour due stress caused by trapping and handling. I divided the dataset into spring (April-May) and fall (August-October) seasons.



### ***Fix rate performance***

I analysed fix rate performance by comparing the total amount of fixes with  $\text{HDOP} \leq 4$  for each animal to the number of potential fixes (potential number of fixes = 4 fixes per hour \* 12 hour period \* the amount of days in the dataset).

### ***Territory size, overlap and nightly distance travelled***

Territory sizes were calculated by three methods, based on Minimum Convex Polygons (MCPs) and Kernel Density Estimators (KDE) (figure 3). I utilised a fixed kernel density estimator to calculate territory boundaries and core areas. This kernel density estimator can be seen as a 3D relief that creates a top in the area with higher density of locations; the kernel function determines their shape and the smoothing parameter their width, in cases where animal locations are dispersed the density estimate will be high in those areas where more locations concentrate and low in areas where there are few (Barg et al. 2005). Using Ranges 7 v2.9 (Anatrack Ltd.), I calculated 95% and 50% isopleths for KDE, and established the territory boundaries at the 95% isopleth in order to remove outliers, sizes were then expressed in square kilometres. The 50% isopleth was calculated in order to analyse differences in core area sizes, this results were compared to the 50% MCPs polygons. When calculating KDE I used the fixed kernel method with a standard smoothing factor given by the program. Autocorrelation of the data was not taken into account since kernel estimators do not require independence of fixes. In the case of the MCP measurements, autocorrelation does not affect the validity of the result because the sampling interval is relatively constant (de Solla et al. 1999). MCPs were calculated using the same datasets as for the KDE in Ranges 7. MCPs territories were measured as the total area encompassed by connecting the outermost locations of the datasets. I utilized the 95% MCPs to be able to remove outliers. Beavers occasionally traverse adjacent territories, such incursions (“sallies”) were present in one dominant male and in 3 of the sub-ordinates’ locations and were excluded automatically by Ranges as outliers. Based on MCPs territory boundaries I calculated territory sizes as the total amount of river bank length that fell inside the resulting polygon. This was done in order to be able to compare the accuracy of my results with other VHF tracking based beaver studies. Nightly distance travelled was calculated in ArcMap 10 (ESRI, Redlands, CA) and expressed as the sum of all straight-line distances between successive fixes. Overlapping of territories was measured in ArcMap10, I generated new polygons where two territories overlapped and expressed their size as a percentage of the total area of each territory.

### ***Activity patterns and seasonal differences***

To detect seasonal differences between sexes I analysed variations in activity for the period between 19:00 and 7:00. I counted the amount of fixes for each individual at every hour for each day of the dataset and calculated the proportional mean for all males and females for each season.

### ***Statistical analysis***

I used the softwares R version (2.12.1) (The R project, <http://www.r-project.org/>) and Analyse-it for Microsoft Excel (version 2.20) (Analyse-it Software, Ltd. <http://www.analyse-it.com/>; 2009). I used pairwise t-tests to compare territory estimates based on KDE and MCP estimators, and Mann Whitney U tests to compare differences in territory sizes between the sexes. I used an independent samples t-test to compare river bank length between sexes, and a generalized linear mixed model (GLMM), with a Poisson data distribution, to examine differences between the sexes in the distance travelled per night. I included individual identity as a random effect and I used the following explanatory variables: sex (binomial, with female = 0 and male = 1), body mass in kg (range 21.4 – 28.5 kg), season (binomial, with fall = 0 and spring = 1), and length of the period of transmitter deployment (range 7 – 24 days). I did not test for interactions because of the low sample size and to avoid model over-fitting. The least significant terms were excluded in a backward stepwise manner until the final model consisted of only significant terms ( $P \leq 0.05$ ). Model evaluation was carried out following the protocol by Zuur et al. (2009). I also used one-way ANOVA to analyse differences in activity between sexes and between seasons.

### **Results**

I deployed the archival GPS units for an average period of  $12.7 \pm 4.3$  (SD) days (range 7 – 24 days). In total 18 dominant animals (7 F and 11 M) (mean  $\pm$  SD weights; males =  $23 \pm 1.1$  kg, females =  $24 \pm 2.3$  kg), and 4 sub-ordinates (2 F and 2 M) (males =  $15.2 \pm 1.7$ ; females =  $18.75 \pm 5.3$ ) were tagged in 17 territories (Figures 4, 5 and 6). In total 14 individuals were captured in the period between April-May and 8 individuals between August-October. In three territories both dominant individuals were trapped, and in two of those territories both dominants individuals were trapped in different seasons.

### *Fix rate performance*

The total amount of locations obtained averaged  $443 \pm 41.1$  (range 190 – 811) per individual before correcting for HDOP; after correction the locations mean was  $356 \pm 35$  (range 158 – 682), and in total 79.6% of locations were between 0.1 and 4 HDOP (Table 1). Overall fix rate averaged 56.6%.

### *Territory size*

Paired samples t-test results comparing MCPs and KDE estimators were for 95% cores ( $t = 1.860$ ,  $df = 21$ ,  $p = 0.077$ ) and for 50% ( $t = -2.557$ ,  $df = 21$ ,  $p = 0.018$ ) showing no difference in territory measurements for the 95% cores and a significant difference in the 50% cores measurements.

Median territory size estimated with MCP 95% was  $0.67 \pm 0.34$  km<sup>2</sup> (range 0.28 – 1.15 km<sup>2</sup>) for males and  $0.60 \pm 0.28$  km<sup>2</sup> (0.28 – 1.03 km<sup>2</sup>) for females. Median territory size estimated with KDE 95% was  $0.54 \pm 0.28$  km<sup>2</sup> (0.17 – 0.98 km<sup>2</sup>) for males and  $0.57 \pm 0.3$  km<sup>2</sup> (0.19 – 1.07 km<sup>2</sup>) for females. I found no difference in territory size between the sexes based on the MCP 95% estimator ( $U = 33$ ;  $p = 0.618$ ) and KDE 95% estimator ( $U = 37$ ;  $p = 0.892$ ). Median sizes of the core areas measured with KDE 50% was  $0.13 \pm 0.09$  km<sup>2</sup> (0.04 – 0.34 km<sup>2</sup>) for males and  $0.15 \pm 0.09$  km<sup>2</sup> (0.03 – 0.28 km<sup>2</sup>) for females. Median size of core areas measured with MCP 50% was  $0.09 \pm 0.08$  km<sup>2</sup> (0.02 – 0.30 km<sup>2</sup>) for males and  $0.12 \pm 0.07$  km<sup>2</sup> (0.04 – 0.26 km<sup>2</sup>) for females. I found no difference in territory size among the sexes using both estimators (KDE 50%,  $U = 36$ ,  $p = 0.821$ ; MCP 50%,  $U = 30$ ,  $p = 0.441$ ).

Mean territory size estimated by riverbank length was  $4.2 \pm 1.4$  km for males and  $4.1 \pm 1.5$  km for females, subordinates had  $3.6 \pm 1.4$  km. I found no significant differences in territory length among the sexes ( $t = 0.147$ ,  $df = 16$ ,  $p = 0.885$ ), between dominant males and subordinates ( $t = 0.966$ ,  $df = 13$ ,  $p = 0.352$ ), and between dominant females and subordinates ( $t = 0.533$ ,  $df = 9$ ,  $p = 0.607$ ).

### *Distance travelled*

The median nightly distance travelled was  $4133.5 \pm 1014.7$  m (3241 – 5843 m) for males and  $4434 \pm 1251.5$  m (3581 – 6891 m) for females, and I found no significant differences among the sexes ( $U = 29$ ,  $p = 0.390$ ).

I found no significant variable explaining the distance travelled by night in the GLMM; the variables were removed from the model in the following order: weight ( $\beta = -0.036$ ;  $p =$

0.303), day's dataset ( $\beta = -0.02$ ;  $p = 0.184$ ), sex ( $\beta = 0.09$ ;  $p = 0.361$ ), and season ( $\beta = -0.16$ ;  $p = 0.11$ ).

### *Territory overlap*

All territory estimates based on KDE 95% overlapped with neighbouring territories. Male territories overlapped on average  $8.83\% \pm 8.46\%$  with both female and male neighbours; and female territories overlapped on average  $6.17\% \pm 5.22\%$  with both male and female neighbours. Mated pairs overlapped on average  $84.12\% \pm 4.8\%$ .

The MCP estimator did not show overlap in 10 of the borders, average overlap without those borders resulted in  $17.04\% \pm 15.10\%$  for males and  $13.37\% \pm 13.56\%$  for females and with the non-overlapping borders male overlap resulted in  $10.48 \pm 15.04\%$  and  $7.29 \pm 12.61\%$  for females. Mated pairs overlapped  $88.44\% \pm 10.12\%$ .

Only two territories overlapped at the 50% cores a dominant male and a female subordinate, with KDE measurements resulting in  $8.23\%$  overlapping for the female and  $19.28\%$  for the male. These territories overlapped at 50% cores for the MCPs as well, resulting in  $9.36\%$  for the female and  $10.89\%$  for the male.

### *Activity patterns and seasonal variations*

ANOVA results of the analysis of activity patterns and seasonal variations (figure 7) showed no significant differences, females ( $F = 0.054$ ,  $df = 1$ ,  $p = 0.819$ ) and for males ( $F = 0.00$ ,  $df = 1$ ,  $p = 0.994$ ). No significant differences were found when comparing patterns of activity between sexes in spring, ( $F = 0.00$ ,  $df = 1$ ,  $p = 0.996$ ) or fall, ( $F = 0.059$ ,  $df = 1$ ,  $p = 0.810$ ). No significant differences between sexes was found for the subordinates ( $F = 0.16$ ,  $df = 1$ ,  $p = 0.901$ ).

## **Discussion**

The archival GPS tags deployed in this study provided a valuable dataset of fixes/locations for each of the studied animals. I was able to map individual territories with a high degree of precision and analyse behaviour in great detail. The fix rate obtained is comparable to rates achieved in other GPS based studies (Recio et al. 2011). Hence, GPS can be regarded as a valuable tool for behavioural studies on semi-aquatic mammals such as the Eurasian beaver.

My findings regarding territory size and distance travelled show no significant differences between sexes indicating that Eurasian beavers do not present behavioural dimorphism between spring and autumn seasons during the length of the study. Minimal

territorial overlapping with conspecifics from different colonies indicates that beavers are highly territorial animals and the absence of overlapping in the core areas with other sexually mature individuals from other colonies supports the hypothesis of Eurasian beavers being strictly monogamous (Campbell et al. 2012).

### ***Fix rate and devices performance***

Previous studies on different mammalian species achieved higher rates of fixes but under different topographical conditions, canopy configurations and with higher HDOP filtering standards (Recio et al. 2011). Many factors can have an effect in fix success, making it difficult to compare between studies, such as species behaviour and activity (Swain et al. 2008) and habitat conditions (Hansen and Riggs 2008). The variations on fix rate obtained in this study, can be explained by the species behaviour and habitat, as central place foragers, beavers visit their lodge repeatedly during the night, they also use burrows dug in the riverbank and might spend several minutes submerged foraging underwater thus difficulting fix acquisition (Quaglietta et al. 2012). Many of the locations were in the water suggesting that, when swimming on the surface, the GPS has no impediment in achieving a fix, thus proving that the method utilized to attach the devices was a success. A factor that may affect negatively GPS functioning was when animals were underground for extended periods of time. The devices will attempt to acquire a fix unsuccessfully every three minutes thus emptying or reducing battery life. This is a pre-set that can be fixed through the GPS internal settings but this option was not considered in this study since I could not predict how often and for how long animals will visit their lodges or burrows during the night.

My results and findings regarding the utilization of archival GPS in beavers suggests that the technology is ripe for studies carried in this environment and type of animal. It provided a good insight on how beavers occupy the three rivers and reduced tracking effort and costs drastically. During the study I was able to deploy multiple devices at the same time, making it possible to study different animals at different locations simultaneously with very little effort.

### ***Home range estimators***

The most important role of a home range estimator is to help identify the key aspects that induce an animal or group of animals to establish and use a specific territory. But to specify the actual utilization of an area is difficult given the complexities of ecological systems and the reduced amount of data we can collect (Horne and Garton 2006). Both estimators used in this study are simple and sufficiently close to the true territory usage to make them useful tools for

predicting beaver behaviour. There were specific cases where the area delineated by MCP differed greatly from that of the KDE, specifically where large areas within a territory were never visited, i.e. territories located by lakes. My results suggest that both estimators complement each other in defining territories for this particular species. MCPs function as a simple space delineator outlining the entire area the animals are likely to visit or protect and KDE gives a deeper insight into areas inside the territory with the highest probability to find the targeted animal. Core areas and space utilisation are better understood with KDE (Nilsen et al. 2008) while border dynamics, in this case beaver territory borders are better understood using MCPs. Since it draws a straight line to define an area MCP delineated territories show a clear cut border where residents and neighbouring territories meet, while KDE, depending on the smoothing factor used might tend to overestimate the border resulting in a biased overlapping.

### ***Territory size and nightly distance travelled***

Territory size and nightly distance travelled indicate that there is no sexual dimorphism in beavers. Both females and males defended similar territories and travelled similar distances during the length of the study. Territory sizes measured as riverbank length are similar to those determined for Eurasian beavers in other studies (Males =  $3900 \pm 1514$  and Females =  $3483 \pm 1720$ ) (Herr and Rosell 2004). Single differences in territory size may be attributed to characteristics in landscape composition and resource availability (Campbell 2005), with the biggest territories being those that comprised lakes where the opposite shore is too far from the core areas, thus some individuals seem to compensate the absence of one shore by using a larger area on the shore closest to their lodge.

### ***Activity patterns and seasonal differences***

My results regarding the activity pattern variations suggests a very marked absence of sexual dimorphism. Both sexes' registered similar levels of activity during the entire 12 hours of the recording period, making conclusions about activity/inactivity not possible with this dataset.

### ***Overlapping***

Regarding overlapping, MCPs and KDE performed slightly different; MCPs did not show overlapping in 10 borders while overlapping was present in all territories measured with KDE. The reason for this can be that the smoothing factor used for this study was not appropriate for this kind of measurements, and territory borders might have been overestimated.

The high overlapping percentage for the mated pairs found in this study is also similar to those found in previous VHF-tracking based studies of Eurasian beavers (Herr and Rosell 2004) and other monogamous species such as cape porcupine (*Hystrix africaeaustralis*: 75%) (Corbet & Van Aarde 1996), mahogany glider (*Petaurus gracilis*: 85.9%) (Jackson 2000) and blanford's fox (*Vulpes cana*: 79.9%) (Geffen & Macdonald, 1992). Overlapping of territories between neighbours, was localised at the borders and with no overlapping in the core areas (50% cores) indicating that territorial borders are more flexible than Campbell et al. (2005) suggested. Or, as discussed by Hinsch et al. (2010) the cost of defending the border is more expensive than the potential damage conspecifics might cause, therefore beavers might tolerate intrusion to some degree.

Polygamy or promiscuity is commonly associated to territory overlapping between conspecifics (Komers and Brotherton 1997), in the case of wolverines (*Gulo gulo*) female territories are determined by food availability while male territories are dependent on the distribution of females predicting that male territories are bigger than those of the females (Persson et al. 2010). In contraposition; as a monogamous territorial species, Eurasian beavers show exclusive intra-sexual territorial overlapping in the 50% core areas, suggesting that mate guarding might be an important factor leading to monogamy in beavers and indicating that both sexes share in territory defence (Herr and Rosell 2004, Rosell and Thomsen 2006).

### **Conclusion**

GPS allows for optimal research effort in the field minimising observer disturbance of the study animals and increasing sample frequency. GPS technology helps to derive conclusions about behaviour patterns and resource use, providing an unprecedented ability to quantify animal territory patterns (Markham and Altmann 2008, Cagnacci et al. 2010, Kie et al. 2010, Recio et al. 2011). GPS technology has proven to be a reliable tool for tracking Eurasian beavers, providing sufficient data for behavioural studies. Further utilization of the technology will give deeper insights into the life history of beavers allowing for a better understanding of the species.

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**Table 1.** Fix rate performance overview of  $\mu$ GPS deployed on Eurasian beavers (*Castor fiber*) arranged by territory location for all rivers, before a filtering fixes with  $Hdop \leq 4$ ; days dataset length variation between individuals is explained by difficulties in retrieving the devices and variations on the raw data.

Animal ID	Sex	Colony <sup>1</sup>	Weight Kgs	Season <sup>2</sup>	Days dataset	No of fixes	Fixes $Hdop \leq 4$	No of potential fixes <sup>3</sup>	Percentage of fixes used <sup>4</sup>	Fix rate percentage <sup>5</sup>
Jan Marc	M	Patmos 0	22.1	Fall	13	481	384	624	78.83	61.54
Hanna-Synnøve	F	Patmos 0	23.5	Fall	12	324	257	576	79.32	44.62
Live <sup>6</sup>	F	Patmos 1	15	Fall	10	366	275	480	75.14	57.29
Leigh <sup>6</sup>	F	Patmos 2a	22.5	Fall	9	252	180	432	71.43	41.67
Moses	M	Patmos 2b	24	Fall	13	407	279	624	68.55	44.71
Christina	F	Patmos 3a	28.5	Fall	12	563	459	576	81.53	79.69
Erlend	M	Patmos 3b	21.4	Spring	12	548	446	576	81.39	77.43
Andreas	M	Bråfjorden a	22.5	Spring	13	326	275	624	84.36	44.07
Leslie	F	Bråfjorden a	22.4	Spring	18	811	679	864	83.72	78.59
Moritz	M	Bråfjorden b	25	Fall	12	221	168	576	76.02	29.17
Kjartan	M	Lille patmos	23.5	Fall	8	315	216	384	68.57	56.25
Ida	F	Lille patmos	23	Fall	19	595	383	912	64.37	42
Horst	M	Patmos 5	23	Fall	18	219	171	864	78.08	19.79
Simon <sup>6</sup>	M	Patmos 6	14	Fall	19	677	557	912	82.27	61.07
Jodie	F	Nordsjø 1	24	Spring	14	487	388	672	79.67	57.74

Hazel	F	Gvarv brua lower	21.5	Spring	24	783	682	1152	87.1	59.2
Paddy	M	Gvarv brua lower	23.5	Spring	14	484	375	672	77.48	55.8
Øyvind <sup>6</sup>	M	Gvarv brua mid	16.5	Fall	11	405	371	528	91.6	70.27
Lasse	M	Lunde 2a	22.5	Spring	12	381	325	576	85.3	96.73
Loran	M	Lunde 4a	25.4	Fall	11	468	412	528	88.03	78.03
Maud	F	Lunde 6a	23.8	Fall	13	459	392	624	85.4	62.82
Bram	M	Lunde 6a	21.5	Spring	12	190	158	576	83.16	27.43

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<b>Mean<sup>7</sup></b>					<b>12.7</b>	<b>443</b>	<b>356</b>	<b>652</b>	<b>79.6%</b>	<b>56.6%</b>
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<sup>1</sup> Colonies from Patmos 0 to Norsjø 1 are located in the Sauar River, Gvarv brua colonies are in the Gvarv River and Lunde colonies are in the Straumen River.

<sup>2</sup> Spring = April-May; Fall = August-October.

<sup>3</sup> Potential number of fixes = 4 fixes per hour \* 12 hour period \* the amount of days in the dataset.

<sup>4</sup> Percentage of fixes from the total amount of fixes obtained.

<sup>5</sup> Percentage of fixes from the number of potential fixes vs. number of fixes.

<sup>6</sup> Sub-ordinates.

<sup>7</sup> Mean values for all variables.

Figure 1. Study area location in southern Norway.



Figure 2a. Sirtrack  $\mu$ Gps and VHF transmitter R1910

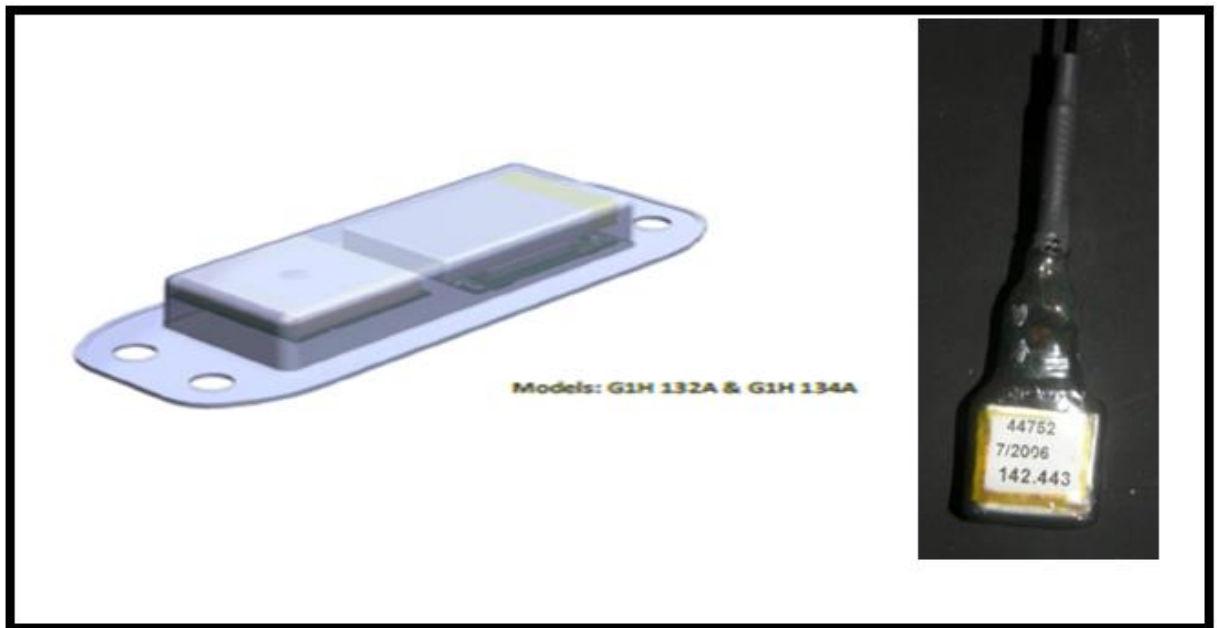


Figure 2b. Eurasian beaver tagged with a GPS and VHF unit being released.



Figure 3. Dominant female territory in Bråfjorden a during the spring season, measured by MCPs 95 and 50% (Hollow polygon) and KDE 95 and 50 % contours (dotted filled), the amount of shoreline that is comprised inside the resulting MCP 95% polygon was measured to calculate river bank length.

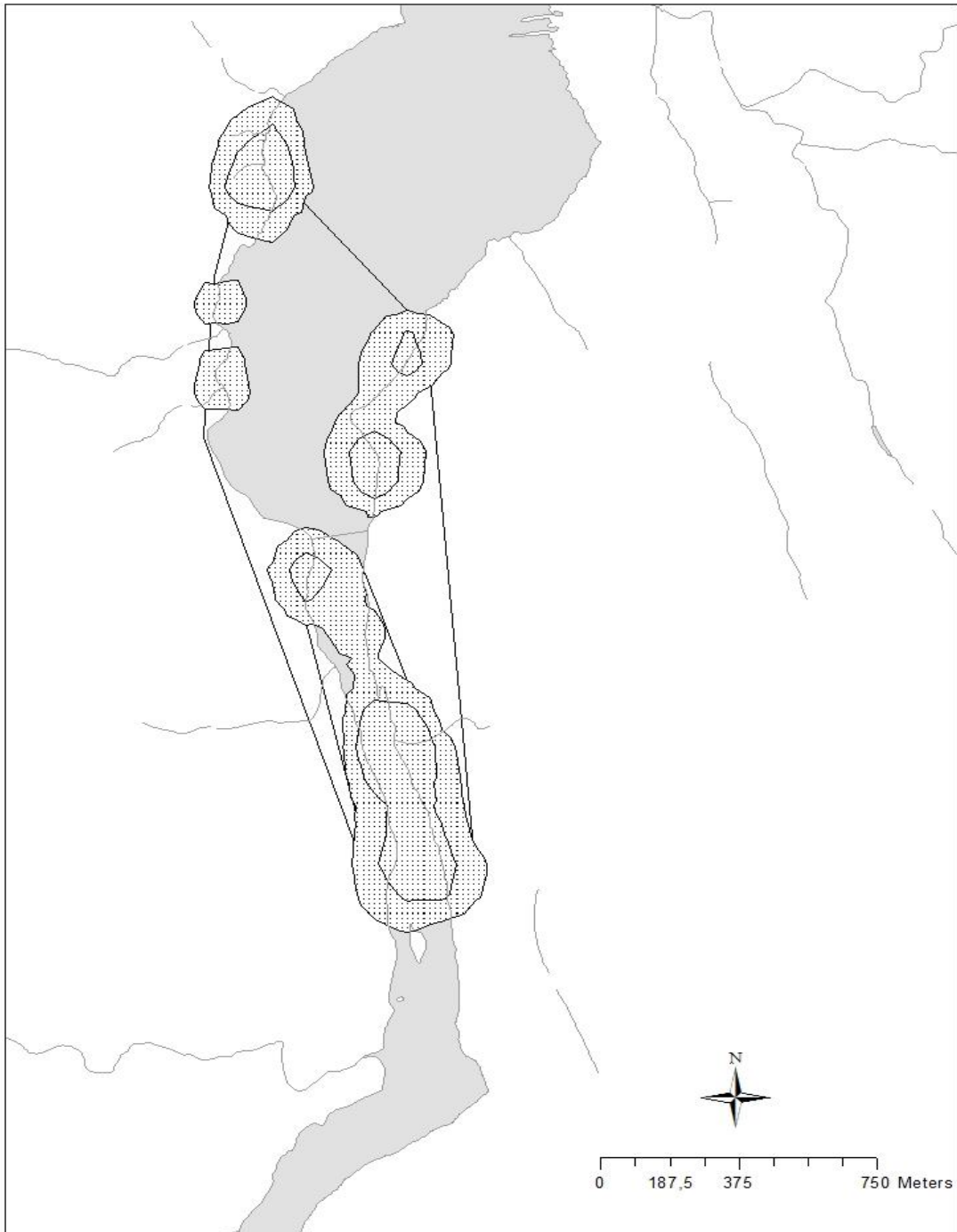




Figure 4. MCP 95% delineating Eurasian beaver territories in the Gvarv River. Black polygons for males and grey polygons for females.

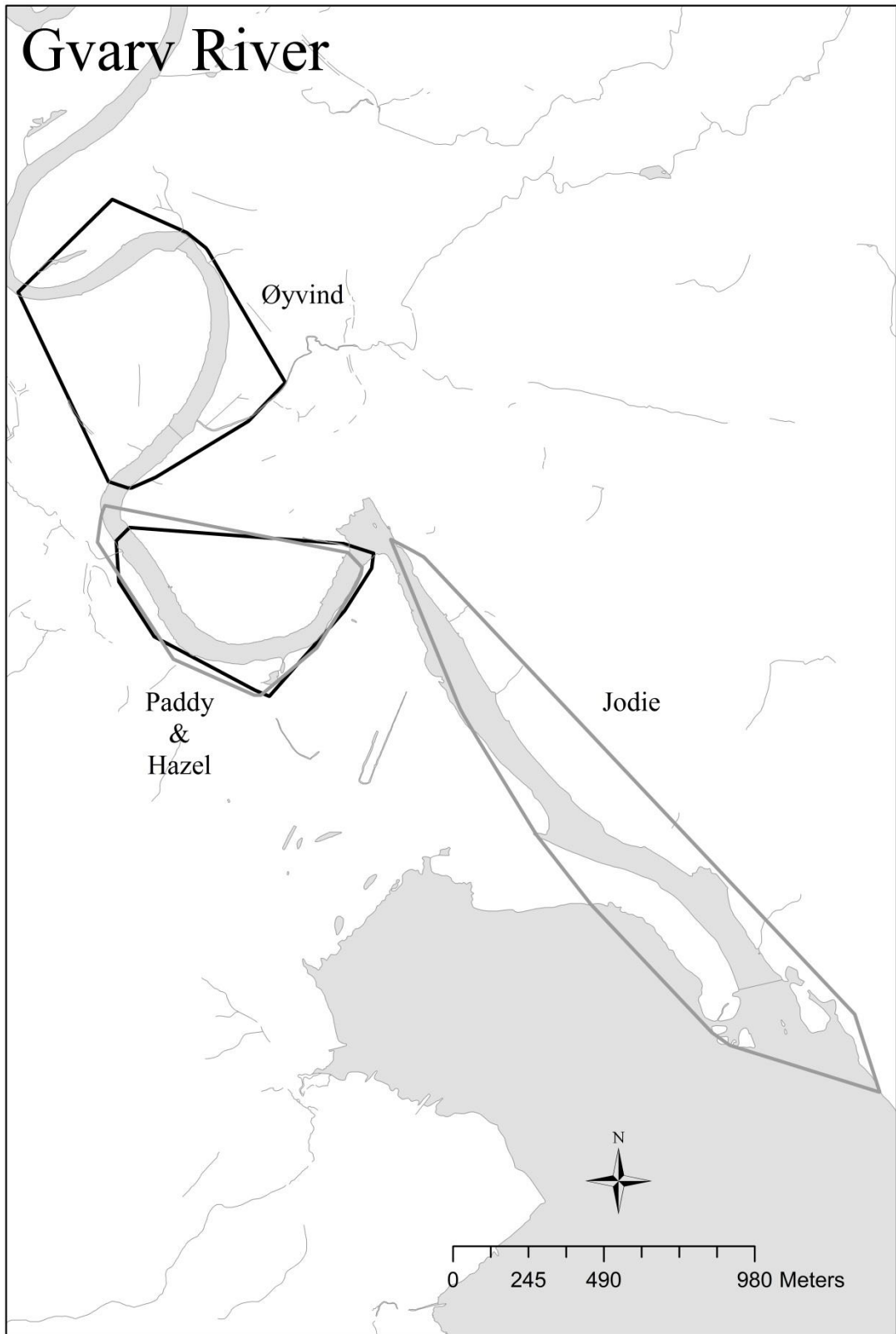


Figure 5. MCP 95% delineating Eurasian beaver territories in the Sauar River. Black polygons for males and grey polygons for females.

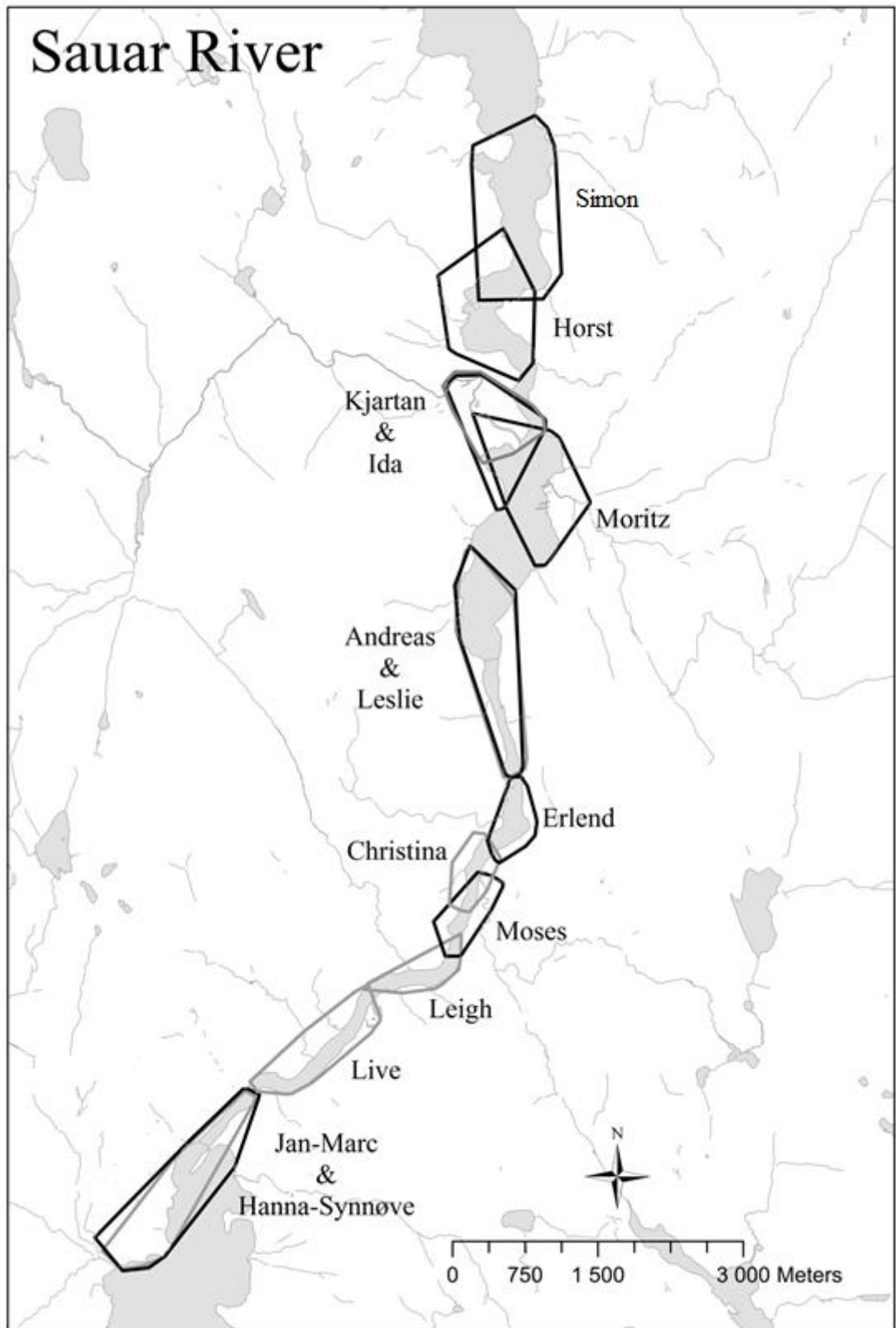


Figure 6. MCP 95% delineating Eurasian beaver territories in the Straumen River. Black polygons for males and grey polygons for females.

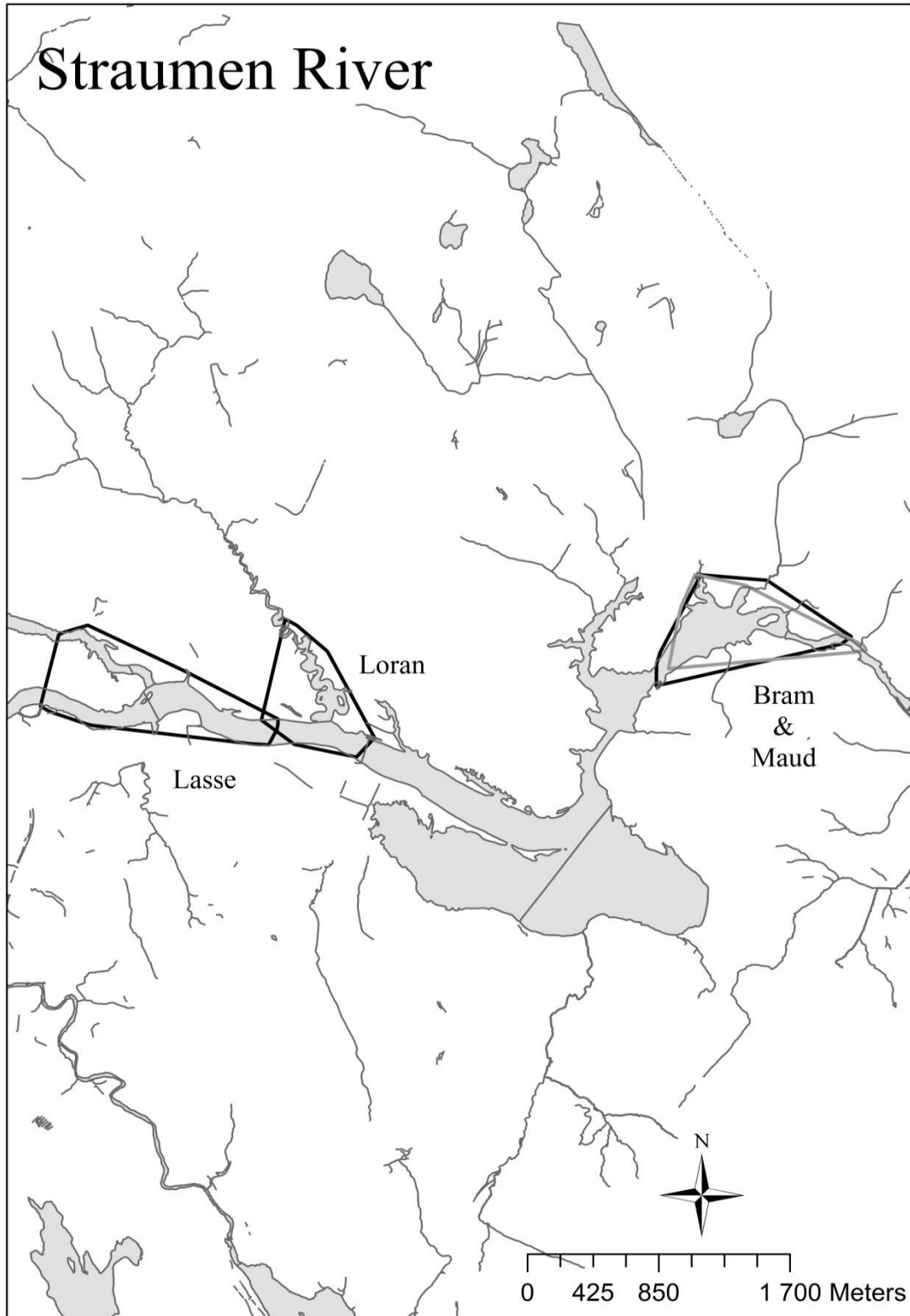


Figure 7. Comparison of activity patterns between sexes and season. Graphics **A** and **B**: Females = Black line and Males = Dotted line. **C** and **D**: spring = Dotted line and fall = Black line. **E**: Females = Black line and Males = Dotted line.

