University of
South-Eastern Norway

Faculty of Technology, Natural Sciences and Maritime Sciences
Master's Thesis
Study program: Environmental Science
Spring 2019

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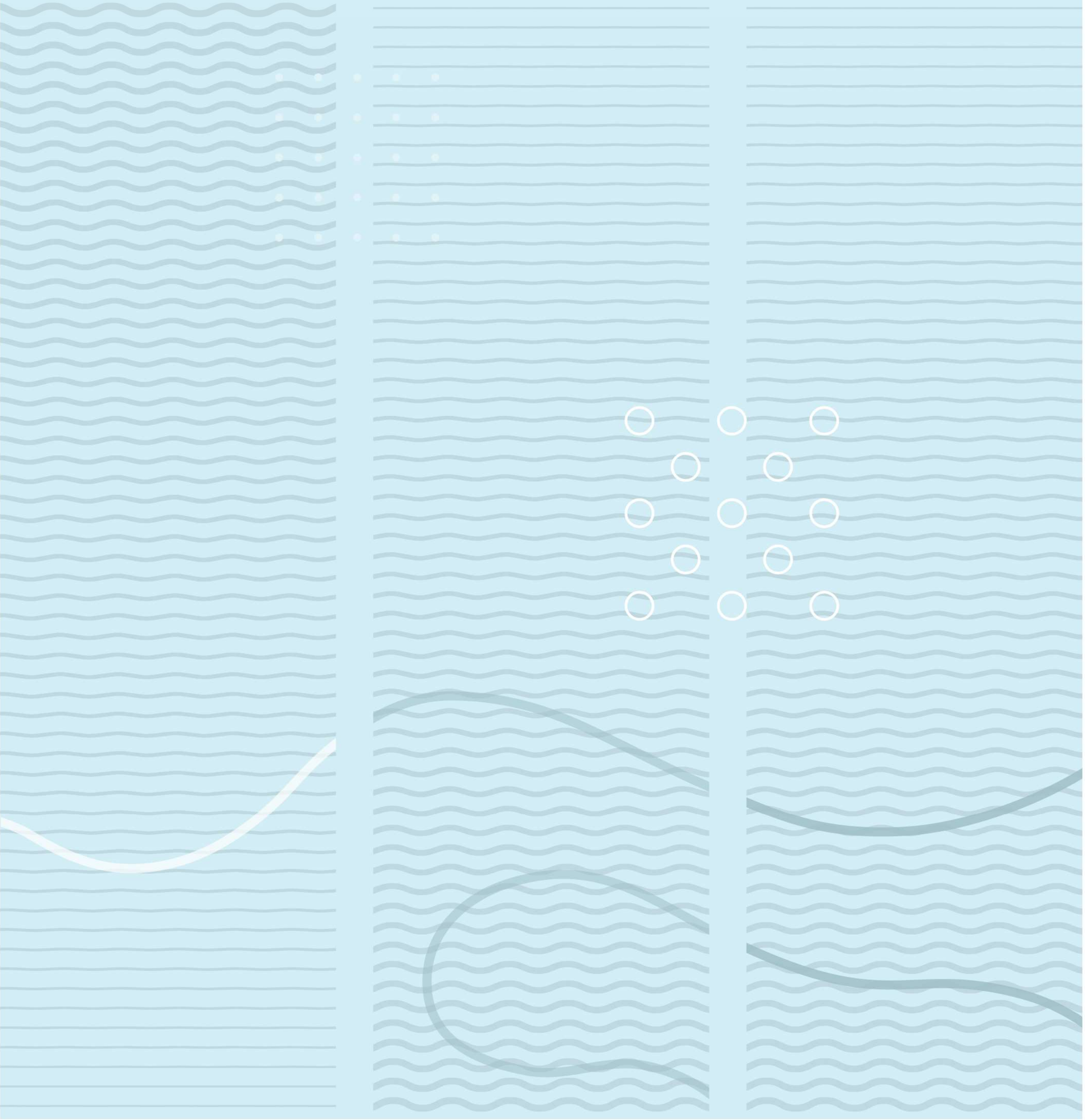
Pair movement of a monogamous mammal, the Eurasian beaver



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Abstract

Studying the cohesion of monogamous pairs is an important component in understanding their social relationships. I used the Eurasian beaver (*Castor fiber*) to investigate how movement patterns and space use relate to their partners in an obligate monogamous and territorial mammal. I analyzed 1984 paired GPS positions from 14 pairs tagged between 2010 to 2018 and calculated the territory overlap of pairs, their distance to each other, and the time spent near territory borders, the main lodge, and in other frequently used clusters. Territory length was of similar size between partners with a high degree of overlap. In addition, more than half of their clusters overlapped although they were rarely located in the same cluster at the same time. Beavers appeared to move independently from each other with relatively large distances between partners (mean ± SD: 480 ± 427 m) that did not differ from their distance to random positions. Beavers in larger territories were overall farther apart, and beavers were the closest at the beginning and end of their nightly active periods when they were also closest to their lodge. They were also closer during the autumn compared to the spring. One partner being in a territory border zone did not influence whether the other one was, although when they were both in the borders concurrently they were more likely to be on the same side. They were also more likely to be on the same side of the territory when not in border zones. Overall, beavers demonstrate low cohesion with their partners which may be a way to avoid predation on multiple family members or to reduce direct competition for resources.

Keywords: Beavers, *Castor fiber,* cohesion, monogamy, patrolling, predation, territoriality

Contents

Acknowledgements

I would first like to thank my supervisor Frank Rosell for all of the support, guidance, and ideas provided throughout my master's project. A special thank you to Martin Mayer for helping immensely with the analysis and providing invaluable feedback on the manuscript. Thank you also to Rasmus Mortensen, Hanna Lodberg-Holm, Alex Briggs, Harry Hirst, and Christian Robstad for all the good times in the field chasing beavers and digging for lost dataloggers, and to Rasmus and Hanna for always being so helpful with my random questions about beavers or statistics. This project has truly been a team effort and I am grateful for the opportunity to be a part of the Norwegian Beaver Project. Funding was provided by the University of South-Eastern Norway.

Bø i Telemark, 15.5.2019
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1 Introduction

Monogamy is relatively uncommon in mammals, with approximately 3-5% of mammal species exhibiting this mating strategy (Kleiman 1977). In socially monogamous species, a single male and female share a common range or territory and form a pair, although they do not necessarily breed exclusively (Reichard 2003). Possible explanations as to the evolution of social monogamy include intense competition between females along with low tolerance of other breeding females (Lukas and Clutton-Brock 2013) and mate guarding by males (Brotherton and Komers 2003). Instances of genetic monogamy in which neither partner breeds outside the social pair are even less common. In birds, less than 25% of socially monogamous species are also genetically monogamous (Griffith et al. 2002), although the rates of genetic monogamy in mammals appears to be more in line with the rates of social monogamy (Lukas and Clutton-Brock 2013). Further, monogamy can be classified as either obligate, when male parental care is required for the rearing of offspring, or as facultative when paternal care is less critical and males may mate with additional females if available (Kleiman 1977).

Monogamy implies exclusivity in social or sexual behavior, yet says nothing of the frequency of interaction, and cohesiveness of pairs can vary widely (Kleiman 1977). For example, pair partners of klipspringers (*Oreotragus oreotragus*) remain within 5 m throughout their life (Dunbar 1984), and kiwis (*Aptelyx australis mantelli*) frequently remain within 50 m of their partners (Taborsky and Taborsky 1991). One benefit of this close association among pairs is the opportunity for the males to guard their mates in an attempt to prevent extra pair copulation (EPC) (Wright et al. 2010), leading to genetic monogamy. In this case high cohesion may predominantly occur during the breeding season (Morrell and Kokko 2005). For example, the red-tailed sportive lemur (*Lepilemur ruficaudatus*) is a monogamous mammal which exhibits low cohesion outside the breeding season, but with a significant increase in time spent near each other when breeding (Hilgartner et al. 2012). The bat-eared fox (*Otocyon megalotis*) maintains close proximity during the breeding season, with some pairs remaining near each other throughout the year (Wright et al. 2010). Conversely, fork-marked lemur (*Phaner furcifer*) pairs exhibit extremely low cohesion even though pairs are stable over several years and their territories overlap almost completely (Schülke and Kappeler 2003), and pairs of elephant shrews (*Rhynochocyon chrysopygus*) are rarely observed together (Rathbun 1979). Maintaining a looser association with their partners reduces competition for resources and allows the individual to independently choose their path of travel (Garber 2000). For example, the fork-marked lemur's low cohesion appears to be a way to avoid feeding competition, as this is their primary source of agonistic interactions (Schülke and Kappeler 2003). Group cohesion can also be a response to predation. One benefit of associating in a group is the reduced rate of predation on each individual due to the added vigilance of other group members and a lower chance of being selected with other prey animals nearby (Delm 1990). However, larger groups also draw more attention, and may increase the rate of attack on the group. For example, African wild dogs (*Lycaon pictus*) are more likely to detect larger herds of wildebeest (*Connocheates taurinus*) and impalas (*Aepyceros melampus*), and are more likely to attack larger herds than smaller herds after detection (Creel and Creel 2002). In elk (*Cervus elaphus*), herd size was observed to increase when wolves (*Canis lupus*) were absent, yet remains small in their presence, indicating that larger groups were not protective from predators (Creel and Winnie 2005). The level of cohesion can also change throughout the duration of a relationship. Giant river otter (*Pteronura brasiliensis*) partners maintain a closer association as the length of their pair bond increases, likely due to increased group stability (Leuchtenberger and Mourão 2008).

Social networks can be used as indicators of social stability which have consequences for an individual's fitness, and can be a useful tool in understanding anthropogenic impacts (Snijders et al. 2017). For example, declines of social cohesion in the killer whale (*Orcinus orca*) coincided with an overall population decline which may be reflective of extrinsic factors such as availability of prey (Parsons et al. 2009). In the Bechstein's bat (*Myotis bechsteinii*), social structure was found to reorganize after a significant population level crash, and previous associations dissolved two years following the crash (Baigger et al. 2013). Changes in social relationships can only be detected if we first understand a population's baseline social structure and the factors on which it depends. Generally, the cohesiveness between the members of a monogamous pair, and especially the underlying spatial movement patterns, have not received much attention or been used in classifying partner relationships. However, Kleiman (1981) has postulated that obligate monogamous mammals should exhibit a stronger pair bond than facultative species, characterized in part by their closer proximity and synchrony of activities. Further, the amount of spatial overlap can provide indirect information about the probability of social interaction (Clutton-Brock 1989).

Both the Eurasian beaver (*Castor fiber*, hereafter beaver) and North American beaver (*C. canadensis*) are large semi-aquatic herbivorous rodents which live in family groups consisting of an adult breeding pair with kits of the year and older non-breeding offspring (hereafter subordinates) from previous years (Wilsson 1971). They are socially monogamous, although approximately 5% of offspring have been observed to have been a result of EPC (Nimje et al. 2018), and both parents are highly involved with the care of the young (Busher 2007). Beavers with kits and/or larger families avoid risky areas associated with human development and spend more time near the lodge, regardless of the sex of the parent (Steyaert et al. 2015). They maintain the same pair bond over multiple years, although mate changes can occur when one partner dies or is forced out of the territory by an intruding beaver (Mayer et al. 2017a). Copulation takes place between January – March, with kits being born around mid-May to June 1st, and emerging from the lodge in July when they begin feeding on their own (Wilsson 1971, Parker and Rosell 2001). The majority of lodge maintenance and winter food caching occurs during the autumn in preparation for winter (Warren 1927). They are highly territorial, with both sexes actively defending their territories through scent marking at territory borders to advertise territory occupancy (Rosell and Nolet 1997) and through aggressive interaction with intruding beavers which can result in serious injuries or even death (Crawford et al. 2015). Beavers in larger territories spend more time traveling and more time within 5% of their territory borders, indicating higher patrolling effort (Graf et al. 2016b). The rate of scent marking has been shown to be positively correlated with territory occupancy time (Rosell and Nolet 1997), and occurs more frequently during the spring when subordinates are dispersing (Rosell et al. 1998). They alert family members to potential danger via tail slapping, which can be heard several hundred meters away (Thomsen et al. 2007). As is typical of monogamous species, they display low levels of sexual dimorphism, both morphologically and behaviorally although males spend more time traveling than females and contribute more to territory defense as evidenced by their higher rates of scent marking and time spent as the border (Osborn 1955, Sharpe and Rosell 2003, Rosell and Thomsen 2006). North American beavers have been shown to engage in few social interactions outside of the lodge and to avoid group foraging (Brady and Svendsen 1981), and to engage in fewer social interactions as they age (Busher and Jenkins 1983). Although previous studies have compared the time budgets of beaver partners (Buech 1995, Sharpe and Rosell 2003, Herr and Rosell 2004), none have observed them simultaneously to be able to include the spatial relationship between them.

The long-term monogamous nature of beaver partners makes this relationship a key component for understanding their overall social organization. I hypothesized that beaver pairs would show low social cohesion. I predicted that 1) beaver partners would have large distance between them, 2) beavers in larger territories would be farther from their partners, and that 3) distance would increase positively with age and territory occupancy time. I also predicted that 4) partners with kits would be closer together due to shared parental care, and that 5) beavers would be closest at the beginning and end of their active periods of the night as they emerge from and return to their lodges, and 6) closer during the autumn when lodge maintenance occurs. Further, I predicted that the use of the territory would be divided, either temporally or spatially (i.e. patrolling the territory at different times or on opposite sides and preferentially using different parts of the territory) to reduce potential conflict for resources, to avoid predation, and to more efficiently patrol the borders.

2. Methods

2.1 Study Area

The study took place in three rivers in Telemark County, southeastern Norway: Straumen (59°297′ N, 09°153′ E), Gvarv (59°386′ N, 09°179′ E), and Sauar (59°444′ N, 09°307′ E), all of which form part of the catchment of Lake Nordsjø (Figure 1). The width of these rivers varies between 20-150 m (Campbell et al. 2012). The climate in this region is cool continental with mean annual temperature 4.6 °C and a mean annual precipitation of 790 mm (Campbell et al. 2012). Due to the presence of natural lakes (Gvarv and Sauar) and weirs (Straumen), which moderate fluctuations in water temperature (Webb and Walling 1996), ice cover is minimal during the winter (Campbell et al. 2012). The landscape is semi-agricultural with farms, fields, and small towns interspersed with riparian mixed-deciduous woodland dominated by Norway spruce (*Picea abies*) and to a lesser degree Scots pine (*Pinus sylvestris*) (Haarberg and Rosell 2006, Campbell 2010). Beavers have been in the study area since the 1920s (Olstad 1937). Beavers do not build dams in this study area as the rivers are wide enough and deep enough to make them unnecessary (Hartman and Törnlöv 2006). The population is considered saturated as beaver territories border each other with no unoccupied areas (Campbell et al. 2005). Pair bond duration of beavers in this study area is on average 4.95 years with an annual mate change rate of about 7% (Mayer et al. 2017a). Hunting and trapping pressure is low (Haarberg and Rosell 2006), and few predators are present in the area as wolves no longer occur and lynx (*Lynx lynx*) densities are low (Rosell and Sanda 2006).

2.2 Data Collection

and have been captured every year in spring (March-June) and autumn (August-November) since 1997 as part of a long-term monitoring program, with GPS units attached since 2009 (Campbell et al. 2013). Beavers are spotted at night from a motor boat using searchlights, and captured using large landing nets either in shallow water or on land (Rosell and Hovde 2001). They are then brought onto shore and transferred into cloth sacks, which enables handling without the use of anesthesia. Newly captured individuals are sexed based on the color of their anal gland secretion (Rosell and Sun

1999), and aged based on body mass (Rosell et al. 2010). Individuals that are captured for the first time as kits or at one year old are assigned an exact age based on their body mass whereas older individuals are assigned a minimum age of 2 years old when captured for the first time with a body mass between 17 kg and 19.5 kg, and a minimum age of 3 years old with a body mass above 19.5 kg (Rosell et al. 2010). All beavers are marked with a microchip and a unique combination of ear tags for individual recognition (Sharpe and Rosell 2003). Status is assigned to breeding individuals based on multiple capture and sighting events within the same territory and lactation in females (Campbell et al. 2013). Additionally, the location of the main active lodge for each territory is recorded based on observations of the beavers going into and out of the lodge, and the presence of freshly cut branches and food caches.

Tag units consisting of a VHF transmitter (Reptile glue-on, series R1910; Advanced Telemetry Systems, Isanti MN, USA) and a GPS receiver (model G1G 134A; Sir-track, Havelock North, New Zealand or TGB-317/315GX; Telenax, Playa del Carmen, Mexico) were attached by gluing them onto the lower back 15 cm above the base of the tail using a two-component epoxy resin (System Three Resins, Auburn WA, USA) (Figure 2a). This position was chosen to minimize the drag and to be able to obtain GPS fixes while the beaver was swimming as the tag remains above water level. Because beavers rarely dive for longer than two minutes (typically <30 sec) (Graf et al. 2017), and transmitters attempted to acquire a fix for three minutes, diving was unlikely to interfere with obtaining a GPS position. Positions were obtained every 15 minutes from 1900-0700 h, when beavers are active (Sharpe and Rosell 2003). The total weight of the tags did not exceed 1% of the beavers' body weight. Beavers were re-trapped after two to six weeks and the units cut from the fur using a scalpel (Figure 2b). All trapping and handling procedures were approved by the Norwegian Experimental Animal Board and the Norwegian Directorate for Nature Management.

2.3 Data Preparation

The capture night and following night were excluded from analysis due to the short-term effects capture may have on beaver behavior (Graf et al. 2016a). For the analysis, I only included breeding pairs where both members of the pair had been tagged concurrently, although it was not necessary for them to be tagged on the same night. Times were rounded to the nearest 15 minutes and only times which recorded a position for both partners were included to allow for a direct comparison between the partners. To correct for imprecise locations, GPS fixes with a horizontal dilution of precision (HDOP) value > 5 and < 4 available satellites were removed (Lewis et al. 2007). This has been shown to reduce location error from an average of 15.7 ± 21.9 m to 14.0 ± 17.0 m (Schlippe Justicia et al. 2018). To calculate individual territory size, I first calculated a 95% minimum convex polygon (MCP) for each beaver with extra-territory movements (ETM) excluded to avoid over-estimation, then extracted the bank length from these polygons in ArcMap 10.4 (Esri, Redlands, CA USA) (Mayer et al. 2017b). As beavers in this study area remain close to the shoreline (on average < 20 m) (Graf et al. 2016b) this provides a more accurate measure of the territory size than methods such a as MCP or kernel utilization distribution (kernel UD) which would include areas not used by the beaver. However, a 95% kernel UD was also calculated, both for the entire tracking duration as well as for each night, to compare the overlap of the partners' territory use. Additionally, core areas were determined by 50% kernel UD to evaluate whether partners concentrate their activity in different parts of their territory. Because 95% kernel home ranges identify a probability area, where the chance of finding the animal is 95%, they are often used to describe the animal's pattern of territory use (Schülke and Kappeler 2003). Compared to the frequently employed method of MCPs they are better able to cope with irregularities in non-uniformly shaped home ranges, are less sensitive to outlying data points, and requires fewer positions to accurately estimate home ranges (Kernohan et al. 2001).

GPS positions were additionally assigned as either upstream or downstream of the main lodge to determine if partners are dividing their use of the territory. The lodge was chosen rather than the center of the territory because it acts as a mutual starting point from which beavers have the option to travel either upstream or downstream. Locations were additionally divided into three categories: border zones, in proximity to the main lodge, and 'other' for locations that fell into neither of these categories. A 75 m buffer around the territory border was used to define the border locations as Rosell et al. (1998) found the majority of scent mounds within this distance from the territory borders. Since beavers rarely move large distances over land, intrusions into another territory will typically occur through the water at these upstream and downstream borders (Herr and Rosell 2004). I also used a buffer of 75 m around the lodge to define GPS positions in proximity to the lodge (hereafter lodge locations). Although the GPS units do not transmit a signal from inside the lodge (Schlippe Justicia et al. 2018), looking at when they are in the vicinity may provide an estimate of when they are entering and exiting the lodge, or times that they remain closer. To identify clusters within the 'other' category where beavers spent a larger amount of time, ArcMap 10.4 was used to create a 15 m buffer around land GPS positions, with areas where at least three locations overlapped considered to be a cluster. These areas are most likely foraging sites as Sharpe and Rosell (2003) found that foraging constituted a significantly larger portion of the beaver's time on land compared with scent marking. The distance between partners was calculated as the Euclidean distance between the male and female at each time GPS positions were recorded for both partners to determine how closely they moved with each other.

2.4 Data Analysis

The size and percentage of overlap between the territories and core areas of male and female territory owner were determined using ArcMap 10.4. Normality of the data was checked using a Shapiro-Wilk test and normally distributed data was compared using a paired t-test. Non-normal data was log transformed, and any set that still failed to reach normality was compared using a Wilcoxon signed-rank test. Pair distance, defined as the distance between the male and female pair member at a given time (dependent variable), was analyzed using a generalized linear mixed model (GLMM) with an identity link. I included the average age of the pair, age difference between partners, territory size, territory occupancy time, reproduction, family size, season, and time of night as fixed effects, and pair ID as random intercept. Reproduction was initially divided into three categories: 'pregnant' if kits were observed in the territory that year and the parents were tracked prior to June 1 when kits are typically born, 'kits' for pairs known to have reproduced and were tagged after June 1, or 'no reproduction' if no kits were observed during the year the pair was tracked, and no yearlings found the following year. However, due to the low number of pairs falling into the 'kits' category (three pairs) and the similar outputs between these and ‘pregnant’ beavers, these categories were combined into one group termed ‘reproduction’.

Collinearity between variables was defined as Pearson correlation values >0.6 and variation inflation factors >3 (Zuur et al. 2010). When correlation was identified I created separate candidate models and selected the one with the lowest Akaike’s Information Criterion corrected for small sample size (AICc) score to be included in the global model (Harrison et al. 2018). I used the dredge function from the package *MuMIn* (Barton 2018) on the global model to identify the most parsimonious model based on AICc. Models with ΔAICc <2 were averaged (Anderson 2007) and parameters were considered uninformative if 0 was included in the 95% confidence interval (Cumming 2013).

To determine if the distance between beaver partners differed from what would be expected if they moved independently of each other I compared their true distance with random positions. To do this I randomized GPS positions for each beaver within the same night and calculated the new ‘random’ distance for each time. I used a GLMM to analyze the pair distance (dependent variable) and included the distance type (true versus random) as fixed effect and the pair ID as random intercept.

To analyze cluster overlap between pairs, a 15 m buffer was drawn around each cluster with any overlapping sites considered to be the same locations. To identify factors that might influence the number of overlapping clusters, I created single-effect candidate linear regression models using the average percentage that each pair overlapped with their partner as the response variable and territory size, family size, average age of the pair, age difference between partners, territory occupancy time, pair duration, season, and reproduction as the fixed effects. I used this average because the number of clusters identified for each pair may be dependent on the number of GPS positions obtained for that pair and single-effect models due to the low sample size (Tripepi et al. 2008). In addition, I calculated the percentage of positions in which beavers were in the same cluster at the same time as their partner.

Territory side use was analyzed using a GLMM with a binomial distribution for each sex with the side the beaver was on as the response variable and side the partner was on as the fixed effect, with pair ID as the random intercept. A separate model was run with whether partners were on the same side as the response variable and age difference between the partners, average age of the pair, and season as fixed effects and the pair

ID as the random intercept. Independence of patrolling was tested for each sex using a binomial model to determine whether beavers are more or less likely to be in the border zone when their partners were. I also included the season, family size, and length of territory occupancy as fixed effects and the pair ID as random intercept. A separate model was run on a subset of pairs that were located in border zones concurrently to determine if they were more or less likely to be on the same side as each other. I ran another binomial model for beavers at the lodge to determine if partners were near the lodge at the same time as each other. I also included season, reproduction, and time of night as fixed effects and pair ID as random intercept. All statistical analyses were performed in RStudio 1.1.463 (R Development Core Team 2015).

3. Results

Fourteen pairs were GPS tagged between the autumn 2010 and spring 2018, with one pair tagged in both autumn 2014 and spring 2015. Four pairs were tagged in the autumn and 11 in the spring. GPS units recorded 9.9 ± 3.3 days of data (range:4-18) and 339.8 ± 155.3 GPS positions (Table 2).

3.1 Territory Size and Overlap

Individual territory sizes ranged from 1114 to 6924 m of bank length (mean ± SD: 2874 ± 1755 m) with no statistical difference between the sexes (Table 3). Male and female territories overlapped with their partners 84.91 ± 10.03% and 90.74 ± 9.80%, respectively. The male had a larger 95% kernel UD, both for the entire tracking period and for each night, with no difference in the 50% kernel UD (Table 3, Figure 3). Male and female 95% kernel UDs for the entire tracking duration overlapped 84.42 ± 13.86% and 95.29 ± 5.76%, respectively. For the 95% kernel UDs for each night, male and female overlap was 56.62 ± 24.85% and 66.59 ± 24.44%, respectively. Fifty percent kernel UD overlap was 61.15 ± 24.35% for males and 77.78 ± 25.41% for females.

3.2 Distance to Partner

The distances to partners observed ranged from 1.1 to 3517.8 m (mean ± SD: 479.9 ± 426.5, median 388.6 m). The true distance did not differ from random locations (Table 4). Distance to partners increased in larger territories as well as during the spring, and was the largest during the middle of their active time (Table 4).

3.3 Locations

3.3.1 Territory Side and Border Zones

Beavers were significantly more likely to be on the same side of the territory as their partners (Z value = 5.3, P < 0.001). Partners with a larger age difference were less often on the same side than partners more similar in age (Table 5). The average distance between partners when both were on the same side was 368.4 ± 346.9 m. Males were in the border zones for a total of 370 positions, accounting for 7.0 to 34.5% of their time (mean ± SD: 18.9 ± 8.0%). Females were in the border zones for a total of 300 positions, accounting for 5.7 to 30.9% of their time (15.4 ± 8.0%). There was no significant difference in the proportion of recorded time that a male and female spent at the border (Paired t-test, t = 1.583, P = 0.136). Additionally, the percentage of time that beavers were at their borders showed a significant moderate correlation with their partners (Pearson correlation, $R^2 = 0.670$, P = 0.006). The presence of one partner at the border had no effect on whether the other was also at the border (Table 5). However, when both partners were at their territory borders simultaneously (65 positions) they were significantly more likely to be on the same side (44 same side; 21 opposite sides: Z value = 2.80, P = 0.005). Males were less likely to be in this zone as family size increased, whereas females were less likely to be in the zone with an increasing territory size (Table 5).

3.3.2 Proximity to Lodges

Lodge locations accounted for 240 out of the 1984 total GPS positions for females (10.9 ± 11.2%) and 215 out of 1984 positions for males (10.2 ± 10.2%). They overlapped for 58 positions, or 16.4 ± 16.2% of the females' time in this zone and 14.1 ± 13.4% of the males' time in it. Beavers were more likely to be in lodge locations when their partner was in this zone (Table 6). Females were more likely to be in the area during the autumn, although the season had no noticeable effect for males. Overall distance to lodges showed a similar nightly pattern as their distance to each other, with them being the closest at the beginning and ending of the active period (Figure 4). Distance to lodge was also lower for reproducing females with no parameters identified as being informative for males (Table 6).

3.3.3 Activity Clusters

Fifty-three clusters outside of the other designated areas were identified for males, and 55 were identified for females, with 34 overlapping (62.9 ± 25.6% of male clusters; 66.3 ± 29.0% of female clusters) (Table 7, Figure 5). No parameters were identified as informative for the number of clusters that overlapped between partners. Males were in these locations for a total of 483 (22.3 ± 12.0%) GPS positions, and females for 516 (26.9 ± 12.3%) of their total positions. Partners were located in the same cluster concurrently for 65 positions (9.3 ± 11.5% of male and 10.2 ± 15.2% of female cluster positions; 3.3% of total positions). Five pairs were never recorded in the same cluster at the same time.

4. Discussion

Overall, the results support the hypothesis of low cohesion among beaver pairs. Although territory size between partners are similar and overlap extensively, there is little evidence that partners coordinate their movement outside of the lodge. Beaver partners appear to be moving independently of each other, neither actively avoiding nor preferentially associating with each other as their distances to each other do not differ from their distances to random locations. However, they were found on the same side of their territories more often than would be expected by chance, although even when on the same side their average distance of almost 400 m is not indicative of a close association. That beavers with larger age gaps were less often on the same side of the territory as beavers of similar age may be reflective of their changing movement patterns as they age. Graf et al. (2016b) reported an increased patrolling effort and time spent on land for older beavers. Although I did not detect an association with age and border use, if beavers are changing their behavior as they age, beavers of different ages may be expected to prioritize different parts of the territory. Further, beavers were observed the closest during the beginning and end of the active period, when they are leaving and returning to their lodge, respectively. This is likely more indicative of their mutual use of this shared space than of their association with each other.

4.1 Territory Defense

Territory size was not significantly different between the sexes. However, males had a significantly larger 95% kernel UD for both the entire tracking duration as well as on a nightly basis. This could be explained by males having more spread out movements, which is supported by previous findings that males spend more time traveling than females (Sharpe and Rosell 2003). This increase in travel time is likely related to territory defense (Nolet and Rosell 1994). Buech (1995) observed that females spent a greater amount of time feeding while males spent more time traveling and concluded that females function primarily as providers of energy whereas males play a larger role in territory maintenance. Due to the energy requirements of producing offspring in female mammals (Gittleman and Thompson 1988), they likely must devote more time to replenishing energy compared to males.

Not surprisingly, partners in larger territories were on average farther apart than those in smaller territories as they have more opportunity to spread out. However, the opposite pattern has been observed in another territorial and sometimes monogamous mammal, the oribi (*Ourebia ourebi).* In larger home ranges, male oribis scent mark less frequently and maintain closer proximity to females, apparently focusing on defending the mate rather than territory in this circumstance, likely due to energy constraints that prevent them from doing both (Brashares and Arcese 2002). No correlation has been observed between beaver territory size and number of scent marks (Rosell et al. 1998), although (Graf et al. 2016b) reported greater relative patrolling effort (within 5% of territory borders) for beavers in larger territories. Thus, unlike the oribi, beavers appear to be focusing their defense on the territory rather than their partners. This is further supported by observations that beavers defend their territories against opposite sex intruders as well as those of the same sex (Thomsen et al. 2007), which would not be expected if beavers were solely guarding their mates (Hilgartner et al. 2012). Two main hypotheses have been put forth to explain the evolution and maintenance of monogamy: the female defense hypothesis (FDH) and the resource defense hypothesis (RDH), in which males monopolize resources rather than directly defending the female (van Schaik et al. 1992). The RDH is expected to occur when females have high energetic demands associated with reproduction (Hilgartner et al. 2012). Ruusila et al. (2000) demonstrated the high cost of reproduction in beavers with their observation that reproductive success is negatively correlated with the previous year’s reproduction. Resource defense may also be a form of paternal care, as decreasing the competition his partner undergoes for food increases reproductive success (Trivers 1972). I therefore conclude that male beavers are defending the territory to secure resources needed to successfully produce offspring.

Beavers appear to be patrolling their territories independently of their partners, as they were no more or less likely to be in the border zones at the same time than would be expected by chance. However, during the times they were both at the border they were more likely to be found on the same side as each other. Additionally, although beavers did not necessarily patrol together, they were in the border zones at similar rates to their partners. Rosell and Thomsen (2006) found that scent marking behavior correlated between mated pairs, showing more similarity with their partners than with other beavers of the same sex. This may result either from both beavers responding to the same external stimuli (e.g. disputes with neighboring beavers) or as a form of mate guarding. In the monogamous klipspringer, males were found to frequently overmark the precise location their partners had previously marked, as an apparent mate guarding strategy (Roberts and Dunbar 2000). However, Rosell and Thomsen (2006) noted that the beavers with the highest rates of marking also appeared to be in the midst of an ongoing territory dispute with their neighbors, lending support to the former explanation. Territorial behavior is an important factor influencing social and mating systems (Hixon 1987) and is expected to evolve when resources such as food and mates are both limited and defendable (Mitani and Rodman 1979). When males and females jointly defend a single territory, this may be conducive with the formation of long-term pair associations, which are indicative of social monogamy (Gillette et al. 2000).

4.2 Resource Competition

Monogamy appears to occur when females are solitary and occupy exclusive territories (Komers and Brotherton 1997), which is largely determined by food availability and distribution (Koenig et al. 2013). Food that is more widely dispersed is thought to promote a ‘scramble’ type competition in which no individual is able to control the resource, whereas discrete patches leads to ‘contest’ competition type (van Schaik 1989). In the Madame Berthe's mouse lemur (*Microcebus berthae*) intense scramble competition was shown to lead to few associations among females (Dammhahn and Kappeler 2010). The pale fork-marked lemur (*Phaner pallescens*) shares the same resources with partners and offspring but avoids direct competition via temporal separation of resource use (Dröscher and Kappeler 2014). Similarly, although more than half of the clusters used by beavers in this study overlapped with their partners, they were rarely located in the same cluster at the same time. Beaver habitat quality in this study area is generally high, with a mean percentage of deciduous riparian vegetation on the three rivers 40.5% and 52% (Pinto et al. 2009). Thus, this resource distribution may be expected to lead to a more dispersed group pattern to reduce occurrences of direct conflict for resources. However, Brady and Svendsen (1981) noted that although North American beavers avoided grouping together while feeding, beavers were able to approach and procure a portion of another beaver's food, yet moved to another area to consume it. Thus, competition is likely not the sole explanation for solitary foraging in beavers.

4.3 Predator Avoidance

As beavers are especially vulnerable to predation while on land and shallow water (Salandre et al. 2017, Gable et al. 2018), solitary foraging may also reduce the rate of predation. Although predation in this area is low, beavers still respond to the scent from predators they evolved sympatrically with equal to those that remain in the area (Rosell and Sanda 2006). Maintaining spacing between beavers may be a way for them to avoid predation on multiple family members (Tinbergen et al. 1967, Brady and Svendsen 1981). Le Roux et al. (2009) compared the foraging strategy between two mongoose species, the yellow mongoose (*Cynictis penicillate*) and the meerkat (*Suricata suricatta*), and found that the solitary foraging yellow mongoose spent more time near boltholes which act as a refuge from predators and were more often under complete vegetation cover. Similarly, beavers often consume their food near water which acts as their refuge from predation (Basey and Jenkins 1995). In addition, unlike the meerkat, yellow mongooses increase vigilance as group size increases, likely due to the higher likeliness of detection by predators (le Roux et al. 2009). When congregating in a group there is a trade-off between increased probability of detection and the dilution effect where each individual is less likely to be preyed upon (Delm 1990). Because beavers live in family groups with genetically related individuals and their mating partners, predation on other members will have a negative effect on their inclusive fitness (Hamilton 1964), negating the benefits of the dilution effect.

Another method of dealing with predation which is facilitated by closer group proximity is the ability to alert other members to danger (Hirth and McCullough 1977). However, in species with a method of communicating over large distances, maintaining close proximity becomes less important. For example, fork-marked lemurs exhibit low cohesion with each other yet still alert other group members with an alarm call (Schülke and Kappeler 2003). The tail slapping alarm employed by beavers (Brady and Svendsen 1981) may play a similar role in maintaining communication with group members without the need to be physically near each other. One of the beaver's primary predators, the grey wolf, hunts beavers by waiting near areas of high beaver use, such as feeding trails, concealing themselves with vegetation or other habitat features, and either immediately attacking them or cutting off their access to water (Gable et al. 2016). With this surprise attack strategy, beavers may not be able to affectively alert family to danger, making it more beneficial to spread out so multiple family members will not be predated on.

4.4 Season and Reproduction

Beaver pairs were closer to each other and to their lodge during the autumn compared to the spring. This is likely the result of both partners taking part in preparing for the winter season with lodge maintenance and food caching (Hodgdon and Larson 1973), which inherently leads to them focusing on the same portion of their territory. It may also be related to the joint care of offspring which are born at the end of spring. Although no pattern was observed for the interaction of season and reproduction (i.e. kits present in the lodge), this may be the result of the low sample size. Steyaert et al. (2015) observed that beavers with kits and/or larger family groups stayed relatively close to the lodge. In another monogamous mammal, the avahis (*Avahi laniger*), pair cohesion was observed higher after birth of their offspring than before (Norscia and Borgognini-Tarli 2008), and proximity with other group members in the stumptail macaque (*Macaca arctoides*) increased after birth (O'Keeffe et al. 1983).

Although no pattern was detected for pair cohesion in relation to reproduction, females with kits were overall closer to the lodge than those without. Although both sexes provide care for their young (Busher 2007), they may primarily do so in different ways. While the female provides direct care by food provisioning and huddling with the young, the male largely contributes in indirect ways such as lodge construction and territorial defense (Busher 2007), particularly after the kits are first born and the male is unable to provide food (Sharpe and Rosell 2003). However, Brady and Svendsen (1981) observed the adult male provisioning the lodge nearly twice as often as the adult female, indicating that he, too, provides care in proximity to the lodge. In addition, they reported that kits most often caravanned from the lodge trailing the adult female, as she remained close to them near the lodge during July and August when they first begin exploring outside. A similar pattern has been observed in other denning mammals: in gray foxes (*Urocyon cinereoargenteus*), mothers reduce their movements by about 80% during the whelping and early weaning periods (Nicholson et al. 1985), and raccoon (*Procyon lotor*) mothers gradually increase their distance from the den as their offspring get older (Hauver et al. 2010).

In addition, the increased distance observed in the spring may be related to differential energy requirements between males and females. For pregnant rodents, mean daily caloric intake increases from 18-25% (Gittleman and Thompson 1988). In the Mendoza tuco-tuco (*Ctenomys mendocinus*), males forage on a significantly higher number of species than females in the winter, but a significantly lower number during the spring when reproduction occurs, likely as a result of the females' increase in energy and nutritional requirements (Silvia et al. 1999). During the spring, reproductive hoary marmots (*Marmota caligata*) forage more in inclement weather and during the night than do nonreproductive females, taking on extra risk to meet their greater nutritional needs (Barash 1980). In beavers, breeding females were found to spend 52% of their active period in May and June foraging, whereas adult males used 29% of their time for foraging (Buech 1995). Parker et al. (2000) compared beavers shot during spring hunting and found that pregnant females tended to be farther from the lodge than other beavers, which may be attributed to them searching for higher quality and more food.

4.5 Other Considerations

It should be noted that I only considered behaviors outside of the lodge in this study, only accounting for half of their time. To fully understand the social cohesion between beaver pairs, interactions inside of the lodge should be taken into account as well. In a study of in-lodge behavior, agonistic behaviors were observed far less frequently than allogrooming, an important method for strengthening pair bonds in mammals (Schino et al. 1988, Mott et al. 2011). However, Patenaude and Bovet (1984) propose that the function of allogrooming in beavers is more likely one of fur maintenance than social bonding as beavers limit the behavior to places that cannot be reached by themselves, its rate of occurrence fluctuates similarly to that of self-grooming, and it occurs in rates approximately proportionally to an individual’s size. In addition, sharing a sleeping site can be useful in classifying group cohesion (Kleiman 1981). In a North American population, beavers within a family did not necessarily sleep in the same lodge when there was no ice present, but overwintered in the same lodge which contained the food cache (Bergerud and Miller 1977). However, sharing a sleeping site may have more practical implications than social. Maintaining the lodge as well as the food cache takes time and energy, so it may be more efficient for both beaves to collaborate on one main lodge. Still, these extensive periods of close proximity to each other cannot be discounted when classifying the beaver’s social structure.

5. Conclusions

Although partners were in some portions of their territories together more often than would be expected by chance, their overall large distances from each other which did not differ from randomly selected positions indicates a low level of interaction. This may be a strategy to reduce predation as larger groups are more likely to be detected, and predation on family members would have a negative impact on fitness. Obligate monogamous mammals rely on the care of both parents, and by defending the territory rather than solely guarding a mate the male can help provide resources which improve the pair's reproductive success. Wey and Blumstein (2010) postulated that adult female yellow-bellied marmots (*Marmota flaviventris*) may demonstrate low levels of social interaction due to their secure position in a colony which they remain in for the duration of their lives. Beaver pairs are similarly stable for long periods of time and therefore may not require substantial amounts of interaction to reinforce their relationship. I have used the location of beavers as an approximation of their activities, however future studies would benefit from the inclusion of accelerometer data to verify how beaver pairs divide their activity time as well as location. In addition, the inclusion on subordinate positions may help to elucidate the dynamic of the entire family group.

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7. Tables and Figures

Table 1. The nine most parsimonious (based on AIC weights) and the full model for the distance between beaver partners. Data was collected on 14 pairs of Eurasian beavers between 2010 and 2018 in southeast Norway.

Model	**Variables**	**df**	**logLik**	**AICc**	**ΔAICc**	**AICc Weight**
1	Season + Territory size + Time + years of territory occupancy	7	-14587.13	29188.3	0	0.145
2	Age difference + season + territory size + time	8	-14586.37	29188.8	0.49	0.114
3	Colony size + season + territory size + time	8	-14586.72	29189.5	1.19	0.080
4	Average age + colony size + season + territory size + time	9	-14585.74	29189.6	1.26	0.077
5	Average age + season + territory size + time	8	-14586.86	29189.8	1.47	0.070
6	Age difference + colony size + season + territory size + time	9	-14585.91	29189.9	1.59	0.066
7	Season + territory size + time + years of occupancy	8	-14586.99	29190.0	1.73	0.061
8	Age difference + average age + season + territory size + time	9	-14586.28	29190.7	2.35	0.045
9	Age difference + average age + family size + season + territory size + time	10	-14585.35	29190.8	2.50	0.042
Global	Age difference + average age + family size + season + territory size + time + years of occupancy	11	-14585.14	29192.4	4.11	0.019

Table 2. Overview of dominant beaver pairs GPS tagged during the spring (S) (March – June) and autumn (A) (August – November) from 2010 to 2018 in southeast Norway.

Pair	Male	Female	Year	Season	Territory Size (km)	Male Age	Female Age	Kits	Family Size	GPS Positions
1	Ivo	Victoria	2016	S	1.199	6	4	No	2	238
2a	Paddy	Hazel	2014	A	2.448	6	11	Yes	5	185
2b	Paddy	Hazel	2015	S	2.424	7	12	Yes	5	65
3	Lasse	Gyda	2015	S	4.681	11	12	Yes	6	86
4	Rory	Malena	2015	A	1.001	7	7	No	4	113
5	Darwin	Laura	2015	S	1.456	5	2	No	2	205
6	Rudolf	Yasmin	2016	S	5.980	6	4	Yes	4	211
7	Jan Marc	Hanne Synnove	2010	A	3.184	6	6	Yes	4	84
8	Morten	Live	2015	S	5.762	6	6	No	7	157
9	Manuel	Apple	2015	S	1.923	6	5	No	6	157
10	Anders	Athena	2016	S	1.333	4	6	Yes	3	109
11	Thomas	Tanja	2015	A	2.115	4	12	Yes	4	146
12	Edwin	Åse	2014	S	3.659	7	3	No	4	97
13	Mini	Nanna	2015	S	1.954	12	4	No	6	89
14	Dylan	Leslie	2018	S	5.578	6	12	No	4	42

Table 3. Comparison of male and female territory size for 14 pairs of Eurasian beavers tagged between 2010 and 2018 in southeast Norway. Bank length was defined by extracting the shoreline from a 95% minimum convex polygon for each beaver. A paired t-test was used when assumptions about normality were met, otherwise data was log transformed and a paired t-test was performed on the transformed data or a Wilcoxon signed- rank test was used if still not normally distributed.

Variable	**Male**	**Female**	**Overlap**	**Test statistics**
Bank Length (km)	3.79 ± 1.68	3.57 ± 1.71	3.17 ± 1.33	t = 1.761; P = 0.099[a]
95% Kernel UD (study duration) (ha)	184.49 ± 111.8	129.04 ± 110.37	123.61 ± 10.33	t = 2.579; P = 0.022[a*]
50% Kernel UD (ha)	33.40 ± 25.72	28.52 ± 28.86	23.32 ± 23.90	t = -1.556; P = 0.142[a*]
95% Kernel UD (nightly) (ha)	41.76 ± 39.73	34.09 ± 38.65	22.26 ± 26.30	Z = -3.100; P = 0.002[b]

* log transformed data
[a] Paired t-test
[b] Wilcoxon signed-rank test

Table 4. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for pair distance to each other from 14 pairs of Eurasian beaver in southeast Norway between 2010 and 2018. I performed model averaging of the best models (ΔAICc < 2) to estimate the effect size of each variable. Informative parameters are given in bold. S = spring.

Variable	**β**	**SE**	**LCI**	**UCI**
Territory Size	**107.106**	**28.531**	**51.154**	**163.057**
Season (S)	**145.074**	**53.367**	**40.355**	**249.792**
Time	**-32.438**	**7.523**	**-47.192**	**-17.684**
I(Time^2)	**1.196**	**0.296**	**0.616**	**1.775**
Age Difference	23.608	18.393	-21.798	35.621
Family Size	-45.492	41.404	-81.636	48.549
Average Age	27.645	26.421	-27.704	40.960
Years Occupied	7.891	14.626	-9.398	10.976
Distance Type (True)	-15.71	12.18	-39.60	8.166

Table 5. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for binomial model of whether beavers were on the same side and within 75 m of their territory borders in southeast Norway between 2010 and 2018. I performed model averaging of best models (ΔAICc < 2) to estimate the effect size of each variable. Informative parameters are given in bold. S = spring.

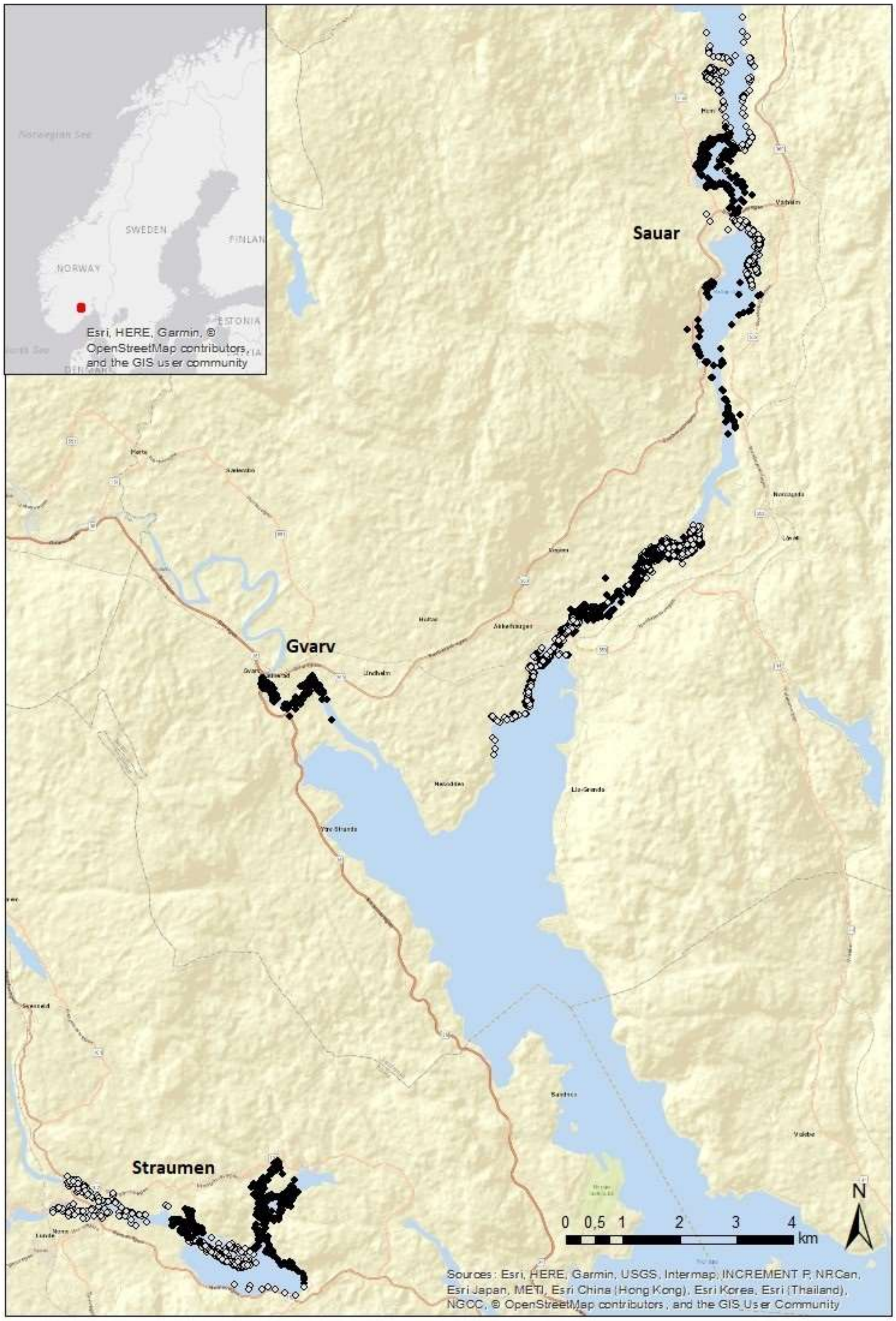
Variable	**β**	**SE**	**LCI**	**UCI**
Partners on the Same Side of Territory				
Age Difference	**-0.114**	**0.051**	**-0.213**	**-0.014**
Average Age	-0.013	0.040	-0.178	0.079
Season (S)	-0.0211	0.108	-0.521	0.324
Males at Border				
Colony Size	**-0.222**	**0.070**	**-0.361**	**-0.084**
Season (S)	-0.181	0.220	-0.613	0.251
Years Occupied	-0.042	0.032	-0.105	0.020
Partner at Border	0.012	0.066	-0.116	0.141
Territory Size	-0.004	0.024	-0.050	0.043
Age	0.001	1.019	-0.036	0.038
Females at Border				
Territory Size	**-0.199**	**0.079**	**-0.354**	**-0.043**
Colony Size	-0.023	0.060	-0.140	-0.094
Season (S)	-0.296	0.283	-0.851	0.258
Years Occupied	-0.336	0.045	-0.122	0.055
Partner at border	0.008	0.053	-0.096	0.112
Age	-0.023	0.042	-0.104	0.059
Reproduction (Yes)	0.320	0.329	-0.325	0.966

Table 6. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for a binomial model of whether beavers were within 75 m of their main lodge as well as their overall distance to their lodge in a population in southeast Norway between 2010 and 2018. I performed model averaging of best models (ΔAICc < 2) to estimate the effect size of each variable. Informative parameters are given in bold. S = spring.

Variable	**β**	**SE**	**LCI**	**UCI**
Males at Lodge				
Partner at lodge	**0.425**	**0.190**	**0.046**	**0.794**
Season (S)	**-1.158**	**0.591**	**-2.535**	**-0.088**
Reproduction (Yes)	-0.192	0.153	-0.496	0.110
Females at Lodge				
Partner at lodge	**0.445**	**0.190**	**0.028**	**0.817**
Season (S)	**-1.369**	**0.435**	**-2.222**	**-0.516**
Reproduction (Yes)	0.127	0.175	-0.216	0.471
Time	0.006	0.017	-0.027	0.039
Reproduction * Season	-0.027	0.128	-0.278	0.224
Male Distance to Lodge				
Reproduction (Yes)	31.544	16.491	-0.794	63.882
Season (S)	-9.003	49.776	-107.454	89.023
Time	0.083	0.210	-0.329	0.496
Female Distance to Lodge				
Reproduction (Yes)	**-37.000**	**15.124**	**-66.656**	**-7.342**
Time	**-0.631**	**0.193**	**-1.009**	**-0.253**
Season (S)	-50.760	46.102	-141.730	39.904

Table 7. The number of clusters identified for each beaver and the number of clusters that overlap with partners. Clusters are defined as areas where at least three GPS positions fall within 30 m of each other.

Pair	Male	Female	Overlap
1	3	5	2
2a	5	3	3
2b	3	4	3
3	3	2	1
4	2	1	1
5	4	4	3
6	5	4	3
7	1	4	1
8	7	8	4
9	6	5	4
10	2	1	1
11	4	4	3
12	3	3	3
13	4	4	2
14	1	3	0
Total	53	55	34



Sources: Esri, HERE, Garmin, USGS, Intermap, INCREMENT P, NRCan, Esri Japan, METI, Esri China (Hong Kong), Esri Korea, Esri (Thailand), NGCC, © OpenStreetMap contributors, and the GIS User Community

Figure 1: Map of the study area in southeast Norway (small map; red dot). Black and grey dots represent locations of 14 pairs of Eurasian beavers from 12 territories GPS tagged between 2010 and 2018.

Figure 2a-b. A GPS unit being glued to a beaver's lower back (a) and removed two weeks later by cutting the fur with a scalpel (b). Fourteen pairs from 12 territories were GPS tagged in southeast Norway from 2010 to 2018.

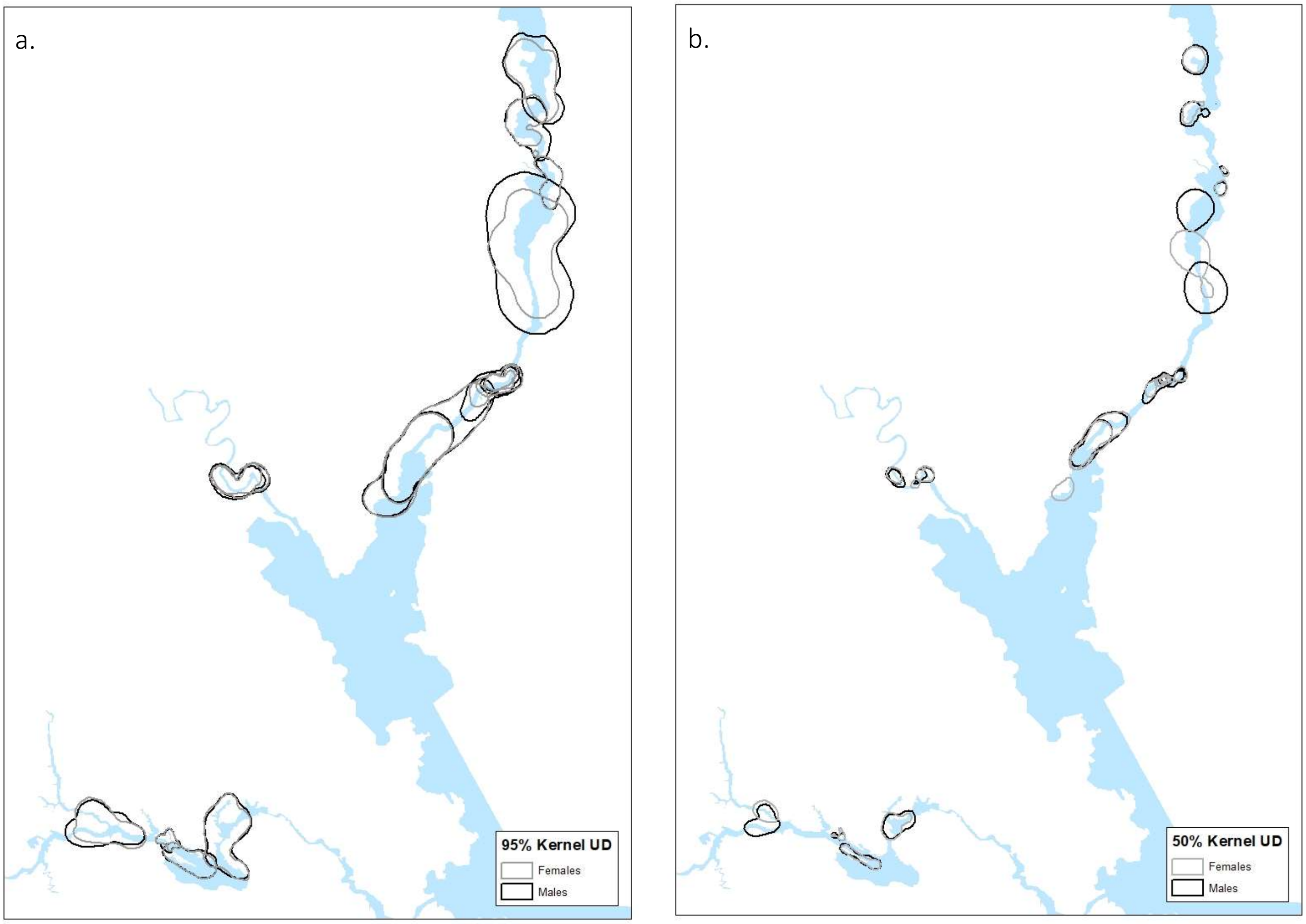


Figure 3a-b. Ninety-five percent kernel UD (a) and 50% kernel UD (b) for 14 beaver pairs GPS tagged in southern Norway from 2010 to 2018.

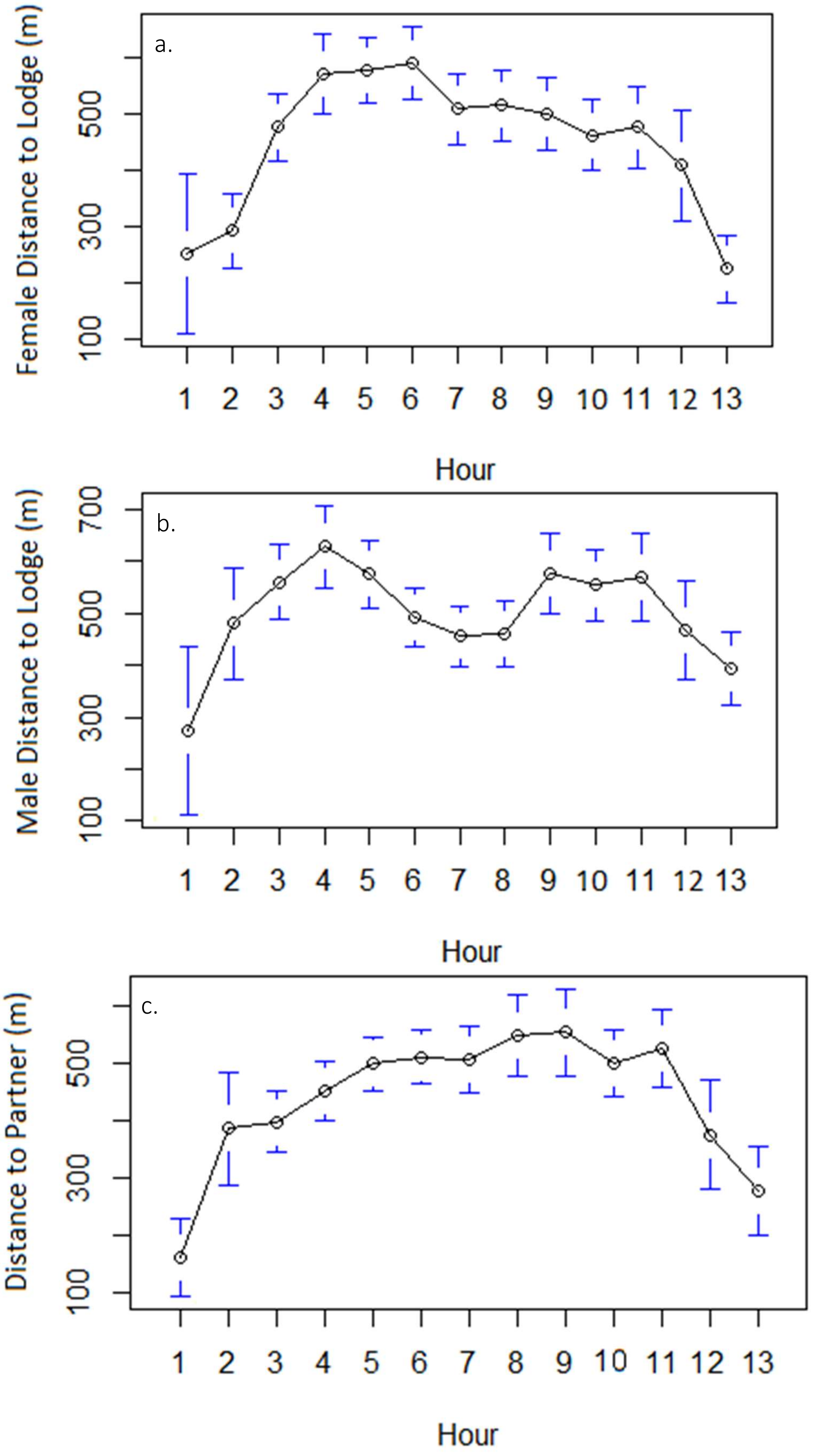


Figure 4a-c. Distance in meters throughout the night between: beaver partners (a), males and the main lodge (b), and females and the main lodge (c). The hour denotes the time since the beavers' active time began and GPS's are set to record a location every 15 minutes (1900-0700).

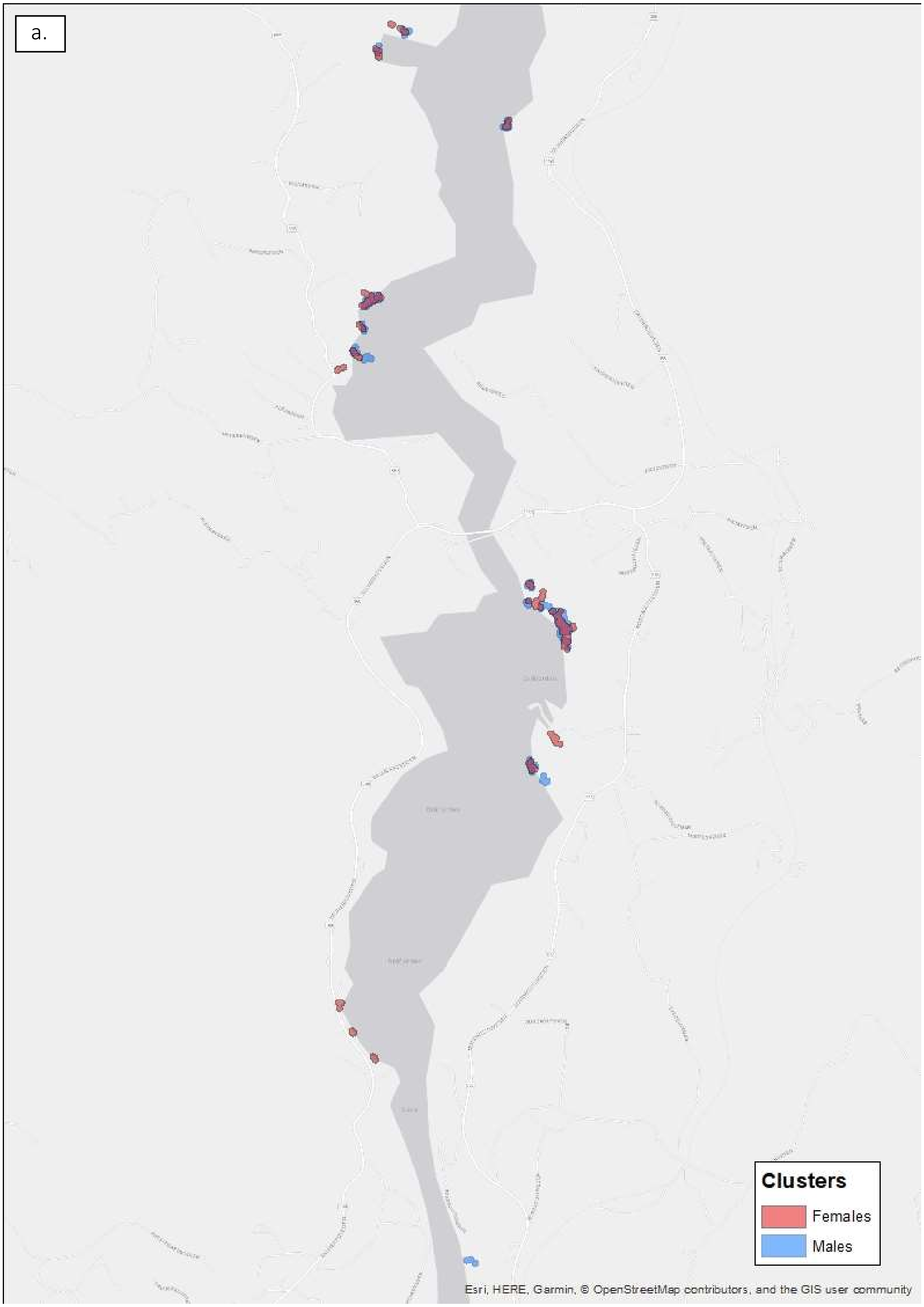
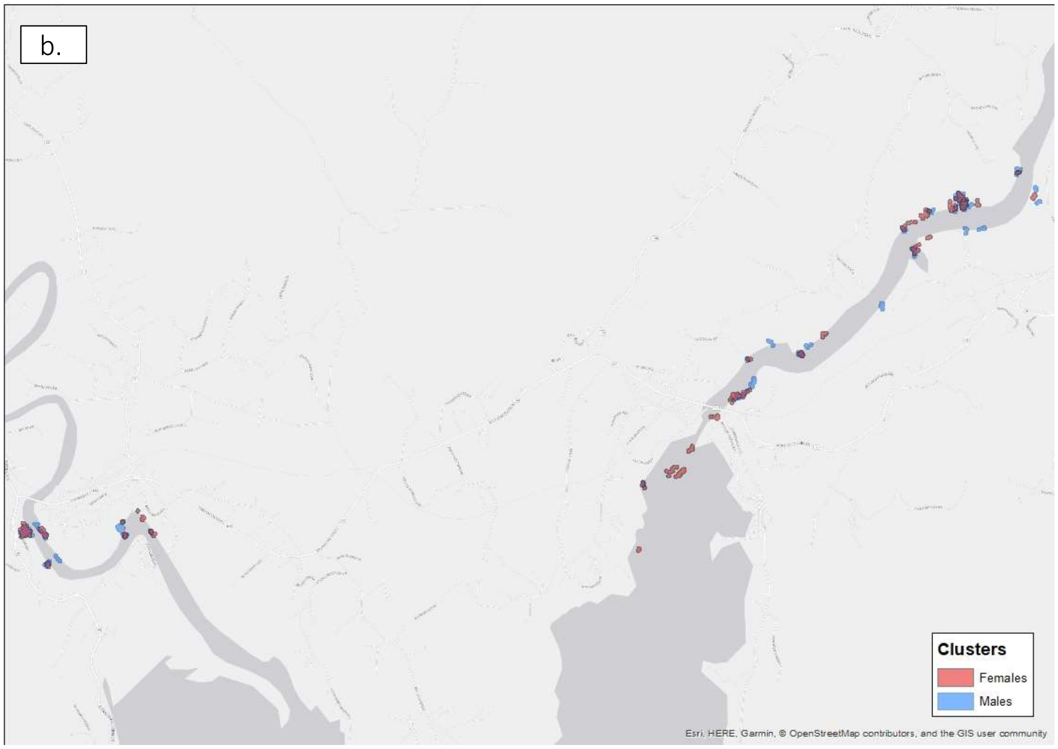


Figure 5a-c. Clusters of ≥ 3 GPS fixes recorded for dominant beavers in southeast Norway in the upper Sauar river (a), the lower Sauar river and Gvarv (b) and Lunde (c) from 2010 to 2018. Males are shown in blue and females are shown in red.


b.
Clusters
Females
Males
Esri, HERE, Garmin, © OpenStreetMap contributors, and the GIS user community


c.
Clusters
Females
Males
Esri, HERE, Garmin, © OpenStreetMap contributors, and the GIS user community