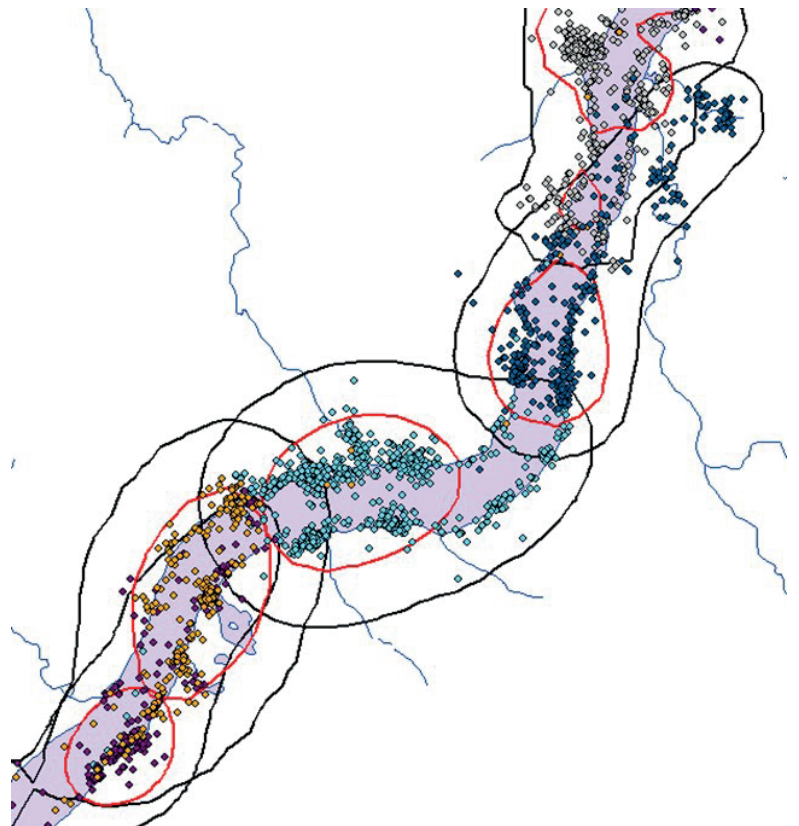


Master Thesis

Anders Mydland

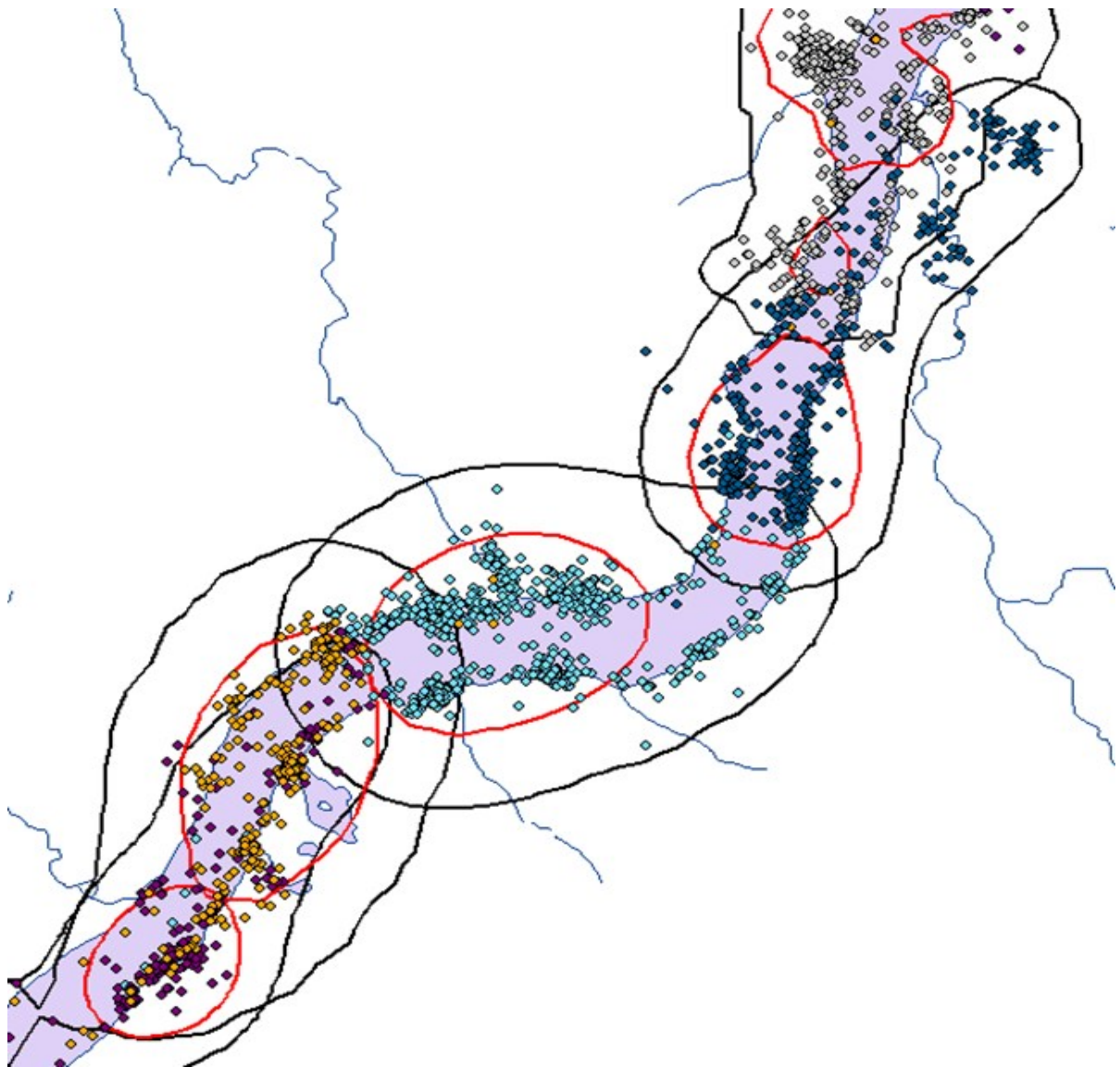
Mapping of sexual and seasonal differences in Eurasian beaver (*Castor fiber*) behaviour using GPS in southern Norway.



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This dissertation represents 60 credits (ECTS)

Mapping of sexual and seasonal differences in Eurasian beaver (*Castor fiber*) behaviour using GPS in southern Norway.

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Abstract

In mammals monogamy is often characterized in mammals by reduced sexual dimorphism. Beavers, being a monogamous species are hard to observe, due to their nocturnal and semi-aquatic nature. In this study I used GPS technology to determine territory size and overlap of the Eurasian beaver (*Castor fiber*). I tested the hypothesis that beavers present no sexual, behavioural dimorphism by measuring activity patterns and territory size. I also predict that there are some differences in behaviour between spring and autumn. Whilst in addition investigating the usefulness of GPS technology in this environment. 27 dominant, territory holding Eurasian beavers, 11 females and 16 males, were fitted with GPS transmitters from 2009-2014. I analysed territory size, territory overlap and activity start and stop times. GPS tags were deployed for an average of 13.1 ± 4.3 days with a fix rate of 15 minutes and territory size was calculated using 95% and 50% Kernel density estimator. My analyses show that beavers do not display behavioural sexual dimorphism. I found significant differences in territory overlap between spring and autumn, with a total overlap of $2.1\% \pm 2.1\%$ in spring and $12.0\% \pm 8.0\%$ in autumn. There were no seasonal differences in the time the beavers emerged from the lodge. However there was a significant difference of the return time. In spring they returned on average at $06:05 \pm 00:44$ whereas in the autumn beavers returned to the lodge at $06:44 \pm 00:44$. These results suggest that beavers do not present sexual dimorphism. In addition my study shows that GPS technology helps us in defining territories and movement patterns with high precision and reducing tracking efforts and costs for researchers.

Key words: beaver, GPS, *Castor fiber*, territory, activity, behaviour.

Introduction

Over the last few decades there have been rapid advances in the range of technology available for biologists and ecologists (Hebblewhite & Haydon 2010). Advances in new biotelemetry (the remote measurement of state variables of individual, free-living animals) methods and technology allows scientists to map the movements of animals, gaining access to vast amounts of detailed data, even for cryptic species (Cagnacci et al. 2010). One of the most useful advances is the use of global positioning system (GPS), which can help ecologists gain a large amount of movement data (Urbano et al. 2010).

GPS systems are repeatable and more accurate than the conventional very high frequency (VHF) triangulation techniques. GPS can have 24-hour coverage and positions may be constantly uploaded (Tomkiewicz et al. 2010). VHF-tracking has a number of challenges that has been overcome by GPS technology. For example; GPS allows data collection in restricted or remote areas, during all weather conditions and maybe most importantly it avoids the behavioural changes of the animal being studied due to the researcher being present in the area. In addition, the movement data from GPS is more precise than data gained from VHF radio signals (Recio et al. 2011). However, GPS also has some significant disadvantages; the devices can be expensive, which can be a problem in itself but this also can make researchers use a smaller sample size. In addition researchers may spend a short time in the study site to attach and remove the devices, which could result in researchers being “divorced” from the field and therefore preventing them from getting the feel of the environment or their study species (Hebblewhite & Haydon 2010).

GPS technology was initially restricted to terrestrial animals large enough to carry the GPS package with batteries (Cagnacci et al. 2010). In 1998 a pilot study was conducted by Douglas Hamilton using GPS collar on African Elephants (*Loxodonta africana*). Two males were collared and over several months their movements were recorded. This study showed that GPS telemetry could provide ranging data important in management planning (Blake et al. 2001). However, over the years GPS technology has become widely available and the GPS devices are getting smaller and in turn increasing the number of animal species they can be attached to (Cagnacci et al. 2010). Ryan et al. (2004) achieved to gain data from small, diving marine animals by attaching GPS devices on African Penguins (*Spheniscus demersus*). Quaglietta et al. (2012) were the first to trial GPS on a semi-aquatic animal that live in a riparian habitat, the Eurasian otter (*Lutra lutra*). They found that GPS is a good tool for diving animals that live in the riparian zone. With this technology it is possible to create huge datasets, which can be used to address behavioural ecology questions from a perspective not

possible a few decades ago such as movement patterns, migration, territories and home ranges (Urbano et al. 2010).

Territoriality is a characteristic displayed by many group-living animals. A territory increases a species reproductive success by supplying it with critical resources, thereby gaining increased fitness (Schradin 2003). Territoriality focuses on the pay-offs between cost and benefits with the size of the territory. Increased territory size means more energy costs to patrol a larger area and higher risk of conflict at the borders, but balanced against this is the benefits of increased amount of resources. The optimal territory size is where the cost-benefit is maximized so the holder of the territory gains the greatest net benefit by defending the territory. However territory economics may not be so clear for group living species (Campbell et al. 2005). Joint territory defence is a common feature for monogamous species and these species usually have reduced sexual dimorphism both on the behavioural and morphological level. The distribution of responsibilities with respect to guarding the territory is usually equal. For example, female tamarins (*Saguinus*) scent mark as often as males and both sexes show aggression against intruders (Kleiman 1977).

Monogamy is somewhat rare in mammals, with only 3% - 5% of all species being monogamous and an even smaller percentage for rodents (Wolff & Sherman 2007). This could be due to males not being as predisposed as females in regard to the care for their young in mammals. Females have a prolonged period of gestation, during this time the male can do little for the young except care for the female and once the young are born, only the female lactates. Due to these constraints, it is not surprising that most mammals are polygynous (Kerbs & Davies 1993). However in some mammalian families, e.g., marmosets (*Callitrichidae*) and foxes (*Canidae*), the most common form of social organization is monogamy (Kleiman 1977). In rodents, two patterns of monogamy emerge; obligate monogamy is thought to have evolved where both parents are needed to care for the offspring whereas facultative monogamy may have evolved in species where the male are unable to gain access to more than one female due to environmental reasons (e.g. widely dispersed females) but is not necessarily vital to offspring survival (Wolff & Sherman 2007). In general, conditions of social monogamy are poorly understood. This has attracted a lot of research attention, mostly because social monogamy is such an unusual system for mammals (Dobson et al. 2010).

The Eurasian beaver (*Castor fiber*) is Europe's largest rodent and the second largest in the world, after the South American capybara (*Hydrochaeris hydrochaeris*). The beaver's body is short and strong and an adult beaver typically weigh between 20 and 25 kg (Rosell et

al. 2006). Beavers are semi-aquatic, nocturnal, strictly herbivorous rodents (Wilsson 1971, Herr & Rosell 2004). They do not hibernate during winter but spend most of their time in the lodge, only exiting to retrieve food that they stored in a food cache under the ice. The food cache is created yearly during the autumn season, this is also the time where most constructing activity takes place (Hartman & Axelsson 2003, Haarberg & Rosell 2006). Beavers live in family groups consisting of a, monogamous dominant pair, kits of the year, yearlings and sometimes subadults (2-year olds). Only the dominant pair breeds in the group (Campbell et al. 2005) and copulation occurs in late January to early February, a time where watercourses are still frozen and therefore copulation takes place in the lodge (Wilsson 1971). It is common for subadults to disperse to the nearest site available, but in high-density populations dispersal is often delayed (Wilsson 1971, Cross et al. 2014). Beavers are territorial and mark their territory with scent marking, which all the members of the group participate in (Campbell et al. 2005). Scent marking has a seasonal peak in spring and is mostly centred at the territory borders (Rosell et al. 1998).

The monogamous, territorial nature of the beaver makes it a suitable model species to investigate the territorial differences between the sexes (Herr & Rosell 2004) as well as seasonal differences. As with most monogamous species, lack of sexual dimorphism makes it hard to visually discriminate between the sexes (Parker et al. 2012). Sharpe & Rosell (2003) investigated whether monogamy has resulted in reduced behavioural sexual dimorphism in the Eurasian beaver. They followed the dominant beavers from six territories by radio tracking. They concluded that time budgets in males and females are similar but not identical, the only difference being that males spent more time travelling than females. This may indicate that males invest more time and energy in territory patrol and defence than females, which in turn may result from males being unable to provide direct care to offspring.

Due to the semi-aquatic and nocturnal nature of beavers, direct observation is difficult. This paper will investigate if GPS can be used to determine beaver territory size and behavioural patterns. I test the hypothesis that beavers, being a monogamous species, present no sexual dimorphism in behaviour and have different activity patterns based on different seasons. By measuring basic aspects as territory size, territory overlap and the start and stop in activity during the night, my predictions were; 1) there are no differences in hours of activity between male and female beavers. 2) There are differences in activity patterns between the seasons of spring and autumn.

Material and Methods

Study area and study animals

The study has been carried out on the Sauar and Gvarv rivers in Sauherad (59°39'N, 9°17'E) and the Straumen river in Nome municipality (59°30'N, 9°11'E), Telemark County, Norway (Figure 1). The climate is cool and wet and for five months a year mean temperature dips below 0°C (Campell et al. 2012). Along their path all the rivers contain lakes, resulting in limited fluctuations in temperature and thus reduced ice cover in winter (Campell et al. 2005). The rivers are wide and deep enough to make dam building by beavers unnecessary (Campell et al. 2012). The rivers flow through an agricultural landscape with mixed woodland. The vegetation along the riverbanks is dominated by gray alder (*Alnus incana*) and lesser extent of rowan (*Sorbus aucuparia*), bird cherry (*Prunus padus*), common ash (*Fraxinus excelsior*), birch (*Betula* spp.), alder-buckthorn (*Frangula alnus*), Norway spruce (*Picea abies*) and willows (*Salix* spp.) (Haarberg & Rosell 2006). There are settlements and scattered houses in the entire study area and the rivers are frequent with boat traffic and leisure activities in the summer. Beavers have occupied the area since the 1920's (Olstad 1937). Hunting pressure in the area is low and the only natural predator present in the area is lynx (*Lynx lynx*) at low densities. The beavers in the study area are part of the long running Norwegian beaver project (NBP) that began in 1998 (Campell et al. 2012). Beavers in the project are marked with colored earmarks and implanted with a microchip, thus I was easily able to select and trap the dominant beavers of each territory from the trapping records (Rosell & Hovde 2001, Sharpe & Rosell 2003) (Table 1).

The study animals were 29 dominant territory holding Eurasian beavers from 20 of a total of 27 territories in the study area. The beavers, 12 females and 17 males, were trapped during the years 2009 – 2014. 6 females and 9 males were trapped in the spring months of March – May and 6 females and 8 males were trapped during the autumn months of August – November. The GPS units transmitted signals for an average period of 13.1 ± 4.3 days (range 6 – 23 days). 3 of the GPS packages were lost during deployment in which one was eventually dug up from a burrow. The 2 others were not found after extensive searching, making the total number of study animals 27 (Table 1).

Methods and Data collection

Dominant territory holding beavers were identified by ear-tags, captured with a landing net from a boat and then immobilized by being transferred head first into a cloth bag (Rosell & Hovde 2001). Once the beaver was in the bag, its ID was confirmed by scanning the

microchip. This method does not require any anesthesia, is quick and has been approved by the Norwegian Experimental Animal Board. None of the animals responded aggressively and none were visibly harmed by the handling. This method has been successfully implemented on beavers in Norway since 1998. The noise from the engine and light from spotlights seems to have little effect on the animals (Rosell & Hovde 2001).

The GPS “package” consists of a micro-GPS device (24g) (model G1G 134A; Sirtrack, Havenlock, New Zealand) and a small VHF transmitter (10g) (series R1910; Advanced Telemetry Systems). The GPS transmit the position once every 15 minutes and is active for 12 hours during the night, from 19:00 to 07:00 o’clock and inactive during the day.

The units were attached to the fur on the lower back of the beaver, 15 cm from the base of the tail with a two-component adhesive. A meshed net secured it from early removal by the animal (Figure 2a). Radio tracking was used to locate the animals for recapture. Without the VHF transmitter, finding the beavers carrying the GPS would have proven difficult and time consuming. Upon recapture the unit was cut carefully out of the fur with a scalpel (Figure 2b). Overall handling time was about 30 minutes and the beaver were released on the site where it was trapped. In cases where recapture proves difficult, the package was eventually groomed out of the fur by the beaver.

Data preparation

Data from the 15 min fixes from the GPS transmitters were used for all analyses. Seasonal differences were examined by dividing the data into two periods, spring (March – May) and autumn (August – November). Prior to analysis, the data was screened for errors in location using the Horizontal Dilution of Position (HDOP) value. HDOP is a horizontal precision estimation of the location, determined by the satellite geometry (Sirtrack GPS receiver user manual). Location fixes from GPS units averaged 405 ± 173.4 (range 146 – 785) before correcting for HDOP. After correcting for HDOP the fixes averaged 370.3 ± 151.4 (range 129 – 701).

Data analysis

GPS data was analysed using GIS-software (ArcMap, Ranges). Territory sizes and territory overlaps were calculated in Ranges 7 v0.811 (Anatrack Ltd.) I used kernel contours (kernel density) (KD) over minimum convex polygon (MCP), because the straight lines of the MCP often include a lot of land in the territory that is not used by the beaver, making the calculated territory larger than it actually is. I used KD 95% to determine territory size by removing location outliers, and KD 50% to determine core area. To evaluate differences in territory size

and activity durations between the sexes and seasons I used a univariate general linear model analysis of variance (GLM). When examining the differences in overlap between the sexes and seasons I excluded 5 individuals, 3 in spring (2 males and 1 female) and 2 in autumn (2 males), due to not having data on their neighboring territories. This analysis was also done with a GLM. I did not use a mixed model due to low sample size. All statistical analyses were done in the program SPSS (IBM SPSS Statistics 22) with a significance level of 0.05 (Field 2009).

Results

Territory size

Mean territory size estimated with KD 95% was 0.57 ± 0.39 km² for males and 0.64 ± 0.26 km² for females with no significant difference between the two sexes ($F = 0.248$, $df = 1$, $p = 0.623$). Mean territory size during spring was 0.68 ± 0.42 km² and 0.52 ± 0.23 km² in autumn with no significant difference between the two seasons ($F = 1.314$, $df = 1$, $p = 0.263$). There was no significant seasonal difference in territory sizes between the sexes ($F = 19.050$, $df = 1$, $p = 0.901$) (Figure 3-5).

Mean core areas estimated with KD 50% were 0.14 ± 0.08 km² for males and 0.17 ± 0.08 km² for females with no significant difference between the two sexes ($F = 0.792$, $df = 1$, $p = 0.383$). Mean core area during spring were 0.17 ± 0.08 km² and 0.14 ± 0.07 km² for autumn with no significant difference between the two seasons ($F = 1.081$, $df = 1$, $p = 0.309$). There was also no significant seasonal difference in core area between the sexes ($F = 0.079$, $df = 1$, $p = 0.781$).

Territory overlap

The mean overlap between territories was $8.3\% \pm 8.7\%$ for males and $5.6\% \pm 6.2\%$ for females. With no significant difference between the sexes ($F = 1.108$, $df = 1$, $p = 0.304$). Mean overlap in spring was $2.1\% \pm 2.1\%$ and $12.0\% \pm 8.0\%$ in autumn, with a significant difference between the two seasons ($F = 15.014$, $df = 1$, $p = 0.001$). There was no significant seasonal difference in overlap between the sexes ($F = 0.849$, $df = 1$, $p = 0.369$). There was no overlap in any of the KD 50% core areas.

Activity start – stop

Mean activity start time for males was $20:31 \pm 00:28$ and $18:46 \pm 05:48$ for females with no significant difference between the sexes ($F = 1.242$, $df = 1$, $p = 0.2284$) and the mean activity stop time was $06:26 \pm 00:44$ for males and $06:24 \pm 00:51$ for females, also with no significant difference between the two sexes ($F = 0.037$, $df = 1$, $p = 0.850$). The mean activity start time in spring was $20:30 \pm 00:40$ and $19:09 \pm 05:08$ in autumn, with no significant difference between the two seasons ($F = 1.333$, $df = 1$, $p = 0.260$). The mean activity stop time in spring was $06:05 \pm 00:44$ and $06:44 \pm 00:40$ in autumn, with a significant difference between the two seasons ($F = 5.792$, $df = 1$, $p = 0.024$). There was no difference in activity start time in the sexes between seasons ($F = 1.845$, $df = 1$, $p = 0.188$) or in the activity stop time between the sexes and seasons ($F = 0$, $df = 1$, $p = 0.999$).

Discussion

This study shows that use of GPS in behavioural studies can be a useful tool for providing valuable and accurate datasets of locations for targeted individuals. With this data I was able to identify an individual's territory size and overlap with neighbouring territories. I was also able to figure out the times that beavers started and stopped their activity during the night.

In all analyses, my results show no differences in behaviour between male and female dominant Eurasian beavers. The small sample size could have resulted in low power, however there is no published data that suggested evidence of behavioural sexual dimorphism in Eurasian beaver, confirming my hypothesis.

Territory size and overlap

The difference in overlap between the seasons supports my second prediction about seasonal differences. Herr & Rosell (2004) found low territory overlap, whereas my results show higher overlap, especially in autumn. The difference may be caused by the different method I used for determining overlap in the analysis. Herr & Rosell (2004) used the VHF tracking method, MCP and riverbank length to determine territory size and overlap whilst I used GPS fixes and kernel density estimator. Already in 1998 the study population was considered to be near carrying capacity, with 18 territories, all having borders on both sides (Rosell & Sundsdal 2001, Rosell & Bjørkøyli 2002). With increase in population density we now have 27 territories in the same study area, resulting in reduced territory size. These new territories have occurred when sub-adults made their own territory by taking a part of their parents area, often pushing the borders of the neighbour on the adjacent side which could explain the increase in border overlap (Cross et al. *in prep*). The difference in overlap between the seasons might indicate that the territories are of different sizes in the spring and autumn. This has been shown in home ranges of brown bears (*Ursus arctos*), where the home range varied with seasonality (McLoughlin et al. 2000). This is difficult to prove as I only have data from one season from each territory. Although in a previous study, Rosell et al. (1998) determined by sight observations, no seasonal difference in territory size but did observe more scent mounds during the spring than in the autumn which may contribute to the low territory overlap in spring. This behaviour is also found in other mammal species. For example, in male ferrets (*Mustela furo*) scent marking peaks in spring (Clapperton 1989) as does the scent marking behaviour of yellow mongoose (*Cynictis penicillata*) (Le Roux et al. 2007). In the Loire valley, the size of beaver territories is directly influenced by vegetation cover (Fustec et al. 2001), suggesting that in autumn, when vegetation cover is degrading in northern latitudes,

beavers are forced to cover a bigger area foraging for food and collecting vegetation for the winter storage. None of the territories I studied showed overlap in the core area.

Activity

Without knowing its behaviour, one can find out if a mammal is diurnal or nocturnal by studying the sight and hearing alone (Ashby 1972). Animals are often nocturnal in order to escape predation (Fichtel 2007).

In terms of activity start time in the nocturnal beaver, there was no difference between seasons but there was a significant difference in the activity stop time between the seasons, in which they stopped their activity later in autumn than in spring, thereby being active for a longer period of time during autumn. Nolet & Rosell (1994) showed that beavers used more time resting in the seasons which have much daylight and Rosell & Hovde (2001) reported that they captured most beavers when it was completely dark, suggesting that activity correlates with the hours of darkness after sunset and before sunrise. A similar pattern was found in sugar gliders (*Petaurus breviceps*), which peaks in activity immediately after sunset and just before sunrise (Kötner & Geiser 2000).

Beavers make winter preparations in autumn. These preparations consist of fixing lodges and dams if damaged and collecting and building up the food cache for the winter (Hartman & Axelsson 2004). Hodgdon & Larson (1973) reported similar behaviour in the North American beaver (*Castor canadensis*). They observed that in the case of lodge maintenance, food cache building and dam maintenance it was the female that did the most work, whereas the male only used more time than female on close dam inspection. Hodgdon and Larsons study was based on sight observations on one beaver colony with marked beavers. However, with a sample size this small, generalizations should be made with caution. These activities combined with longer hours of darkness might explain the extended activity time during autumn.

Conclusion

This study demonstrates that the use of GPS on beavers, as well as other animals, is a reliable method to collect movement patterns without observer disturbance and can provide huge datasets for further studies containing valuable spatial and temporal information. In addition I have found no sexual dimorphism in the activity time budgets of beavers although they do display seasonal differences with regard to nightly activity durations.

Acknowledgements

I would like to thank Aleksander Enoksen for his help in the field as well as Christian Robstad whose expertise in the field made everything just a little easier. Andreas Zedrosser who made statistics a little more understandable and Hannah Cross helped with the English language and kept me motivated. Starting help with GIS from Manuel Echeverria was most appreciated. Lastly I would like to thank my supervisor Frank Rosell for providing invaluable input and guidance throughout the project. The study was financially supported by Telemark University College.

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Table 1: Overview of data collected by GPS deployed on Eurasian beavers (*Castor fiber*) arranged primarily by season and colony. Variations in days of data are explained by raw data variations, battery lifetime and difficulties in retrieving the GPS devices.

Animal ID	Colony ¹	Sex	Season ²	Days of data	Number of fixes	Year	Territory Size KD 95 % (Hectare)	Territory Size KD 50% (Hectare)	Overlap (%) KD95%	Activity Start ⁵	Activity Stop ⁶
Hanne Synnøve	Patmos 0	F	A	13	276	2010	101.9	28.3	0	20:08	05:15
Jean-Marc	Patmos 0	M	A	15	417	2010	96.8	25.7	0	20:23	07:03
Live	Patmos 1	F	A	20	242	2013	39.2	6.5	10,4	01:26	06:37
Manuel	Patmos 1	M	A	10	285	2013	55.8	14.6	24	20:41	06:38
Apple	Patmos 2a	F	A	18	649	2013	53.6	15.8	13,2	19:12	06:47
Moses	Patmos 2b	M	A	15	347	2010	39.7	10	20,7	20:51	06:25
Christina	Patmos 3a	F	A	20	526	2010	38.3	13.7	18	20:48	06:36
Erlend	Patmos 3b	M	A	16	422	2013	10.7	2	25,6	20:05	07:17
Moritz	Bråfjorden b	M	A	8	193	2010	45.4	11.5	14,3	21:37	06:32
Kjartan	Lille patmos 1	M	A	10	277	2010	52.5	10.3	13,2	20:47	05:56
Ida	Lille patmos 1	F	A	15	415	2010	58.7	14.7	10,3	19:52	07:00
Horst	patmos 5	M	A	8	185	2010	51.5	13.3		19:57	06:42
Maud	Lunde 6a	F	A	12	404	2009	52.1	14.6		21:22	08:01
Loran	Lunde 4	M	A	13	412	2009	37.8	9.2		21:02	07:35
Erlend	Patmos 3b	M	S	15	473	2010	17.9	3.3	0,8	20:37	06:46
Leslie	Bråfjorden a	F	S	19	701	2010	69	21.2	0,1	19:58	07:13
Andreas	Bråfjorden a	M	S	9	277	2010	57.6	16.2	0,6	20:39	06:16
Jodie	Nordsjø 1	F	S	13	425	2012	80.8	24.4	0,9	20:32	06:12
Paddy	Gvarvbrua (Low)	M	S	12	415	2012	25.9	8	5	20:21	06:41
Hazel	Gvarvbrua (Low)	F	S	23	684	2010	20.6	6.7	0,2	21:12	06:00
Lasse	Lunde 2a	M	S	11	336	2011	95.1	33.7		20:31	06:23
Bram	Lunde 6a	M	S	8	161	2011	60.6	17.3		20:49	04:16
Klumpen	Gvarvbroa (Mid)	M	S	6	454	2014	18.9	14.3	0	19:33	06:00
Edwin	Patmos 6	M	S	13	194	2014	164.9	21.3	3,4	20:07	06:30

Åse	Patmos 6	F	S	8	385	2014	101.6	14.3	3,8	19:45	05:33
Tanja ³	Patmos 5	F	S	10	129	2014	84.3	22.8	4,6	22:12	05:18
Thomas	patmos 5	M	S	13	313	2014	88.4	14.3	6,2	20:26	06:00
Ikea ⁴	Gvarvbroa (Mid)	F	S								
Lasse ⁴	Lunde 2a	M	S								

¹ Colonies from Patmos and Lille patmos are located in Sauar River, Gvarvbroa and Nordsjø colonies are located in the Gvarv River and Lunde colonies are located in Straumen River.

² A = Autumn (August-November, S=Spring (March-May).

³ GPS lost. Retrieved after located in a burrow.

⁴ GPS lost and not found after searching.

⁵ First emerged from lodge

⁶ Last Return to lodge

Figure legends

Figure 1: Study area location in Sauherad and Nome municipality in southern Norway.

Figure 2a: GPS “package” being attached to beavers lower back using two component glue and meshed net.

Figure 2b Removal of the GPS “package” by cutting it carefully out of the fur with a scalpel, leaving a bald spot on the beavers back.

Figure 3: KD 95% Calculated Eurasian beaver territories in the Gvarv River. Grey lines for spring and black for autumn

Figure 4: KD 95% Calculated Eurasian beaver territories in the Straumen River. Grey lines for spring and black for autumn

Figure 5: KD 95% Calculated Eurasian beaver territories in the Sauar River. Grey lines for spring and black for autumn.



Figure 1



Figure 2a



Figure 2b

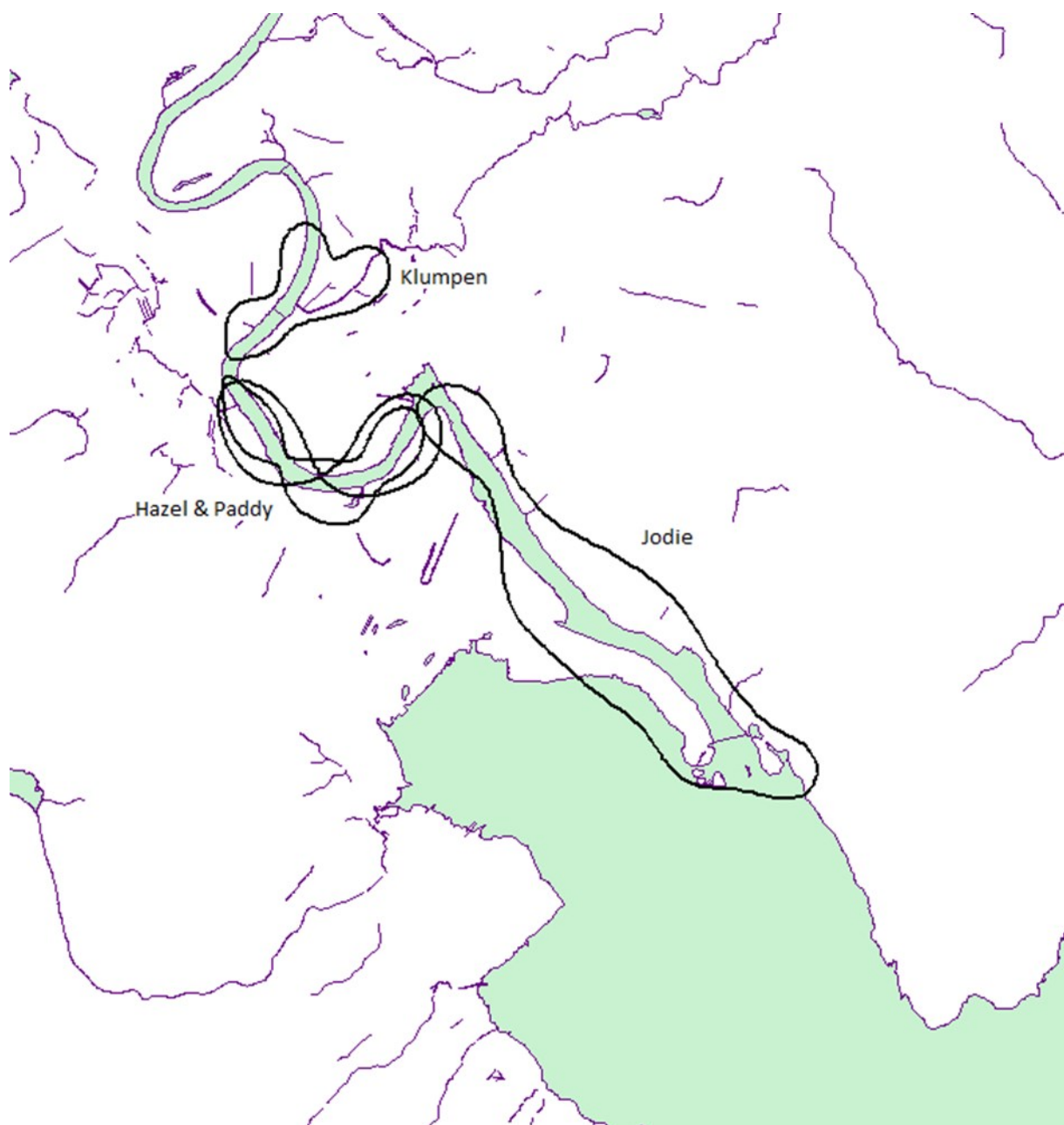


Figure 3

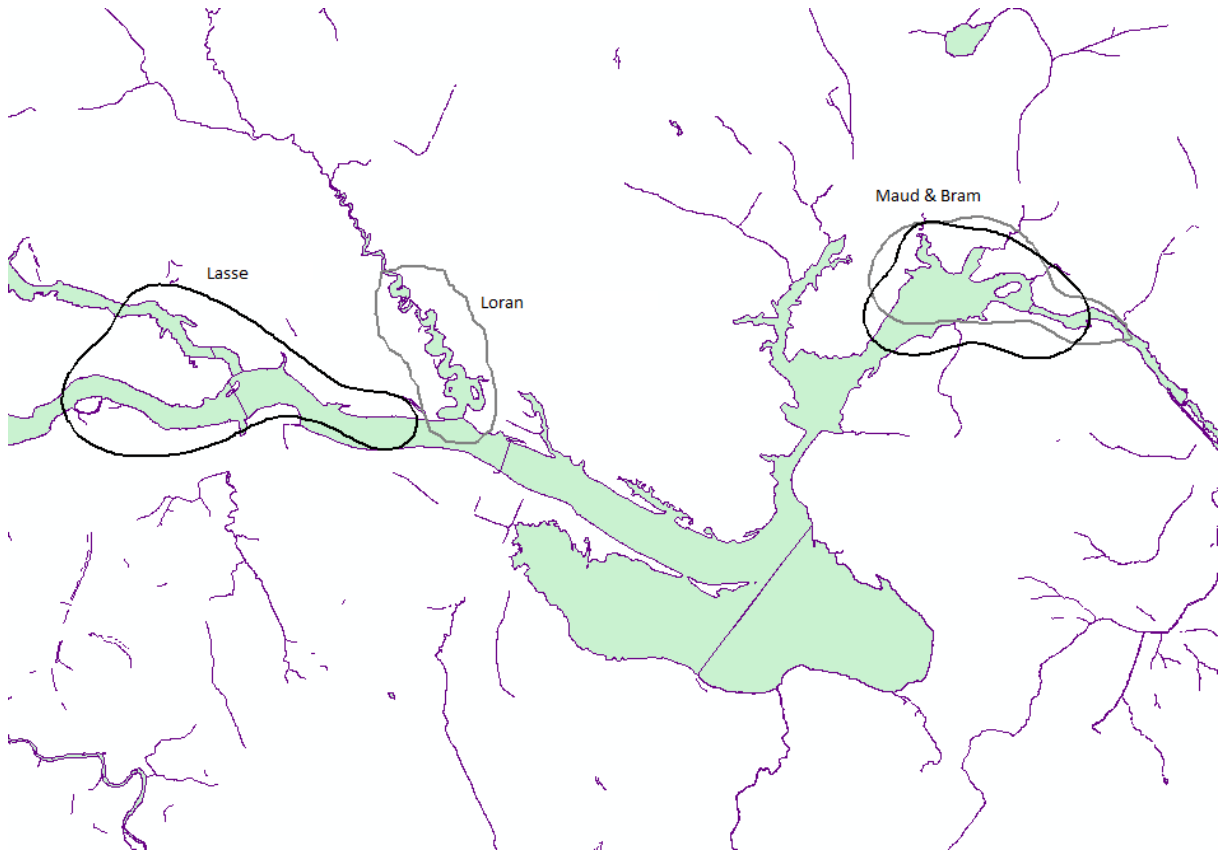


Figure 4

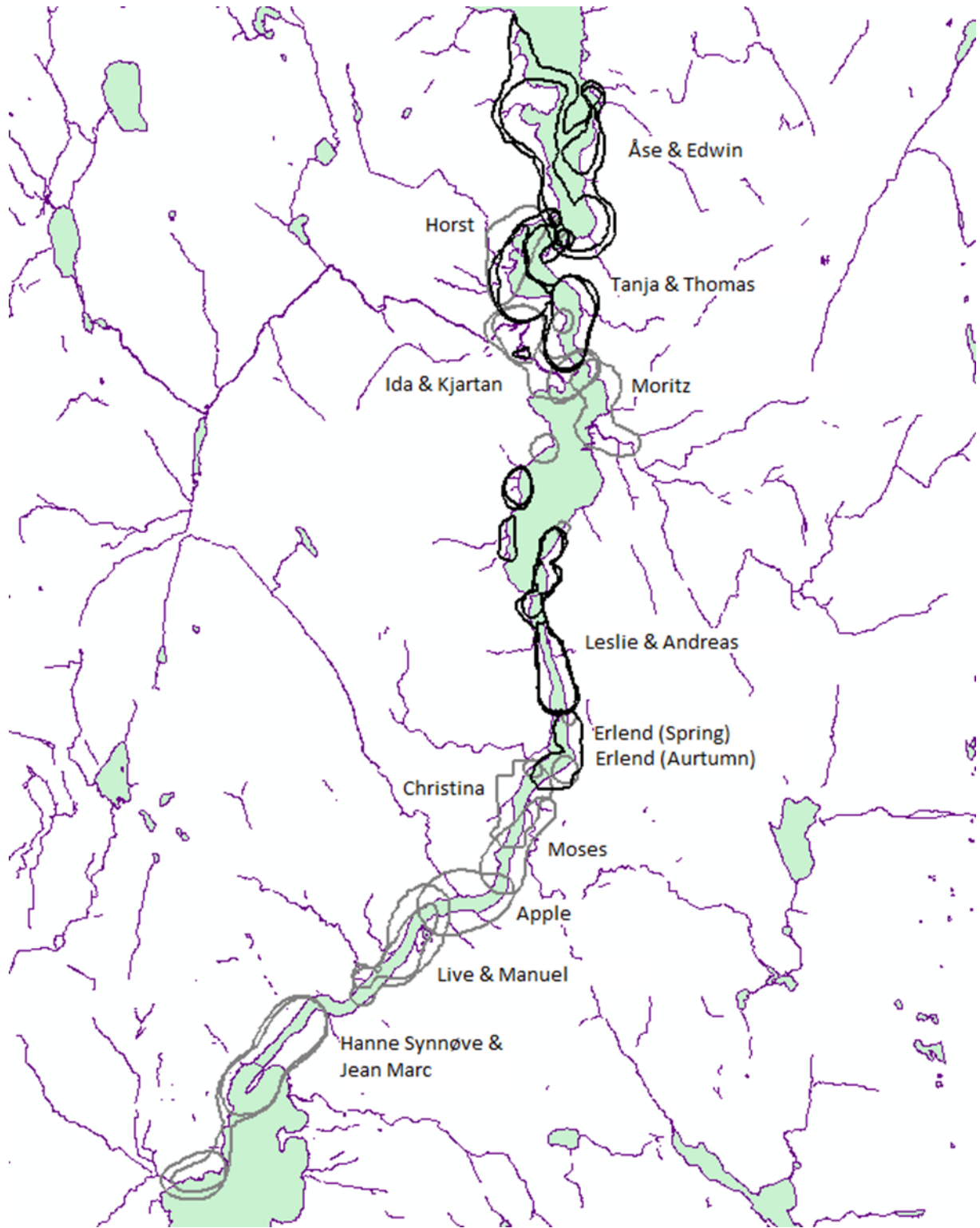


Figure 5