Social structure of brown bear (*Ursus arctos*) in Eastern and Central Finland

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Master thesis 2020
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1. Introduction

1.1 Social structures

Social structure defines an important class of ecological relationship (Whitehead, 1997) that arises since two individuals come into contact with each other. Social structures can have different levels of intensity (Kawata, 1990), often depending on how well developed an animal is. With the help of social structures, groups of animals may improve their chances of survival by gaining food easier or protecting themselves from danger (Whitehead, 1997).

Frequently, complex social structures are observed in some animals that form a community, such as wolf packs, horse herds, or group of whales (Gero et al., 2015; Keiper, 1988; Peterson et al., 2002). Animals that are predominantly solitary often have developed a non-complex social structure among each other (Bellemain et al., 2006a). Nevertheless, social interactions do exist in solitary living animals, as the animals have to come together in order to be able to reproduce, or because of abundant food source that is enough for a large number of individuals (Rode et al., 2006).

Focusing on the brown bear, it spends most of its time solitary but, in a few occasions, it can come in contact with other bears (Støen et al., 2005): One of these occasion could be due accessibility of food sources. For example during the salmon season in Alaska bear density can be very high along a river with good salmon hunting possibilities (Rode et al., 2006). Another occasion is during the mating season, when both female and male adult bears tend to roam to mate (Dahle and Swenson, 2003c). Sometimes copulation takes only a few hours but it has also been observed that bear couples stay together over few days or even a week (Hamer and Herrero, 1990). These examples indicate that social interaction is happening also in brown bears. Nevertheless, just little is known about their social structure.

1.2 Home ranges

Large predators such as wolves, lynxes and wolverines are often territorial species (Smith et al., 2015). They defend their territory from other members of the same species which do not belong to the same pack. The territory provides protection and sufficient amount of food for the individual or the pack (Rich et al., 2012). This is especially necessary in cold regions, as food sources are limited in winter. A territory is used and protected by just one individual or a group of individuals. If the area is not protected by the individual or a group of individuals from the same species other terminologies for land use need to be applied, such as home ranges.

Home range is defined as a living area for an animal in which the animal stays over its lifetime, but which can overlap with other individuals. The publication of Kawata 1990 report in mammals two different home range use for related females which home ranges are overlapping (Table 1). It shows that, apart from environmental conditions, relatedness can have also some effect on the overlap of home ranges (Atwood and Weeks, 2003).

Table 1: Two types of home range overlapping between neighboring females (Kawata, 1990).

Type of interaction	Spatial distribution
Overlap I-kinship	The home ranges of two females overlap. The combined area of the two females contains sufficient resources for rearing the litters of both.
Overlap II-kinship	The home ranges of two or more females overlap. The combined area of the two females does not have sufficient resources for rearing both litters. Just the dominant female is rearing offspring.

1.3 Sampling methods

Collecting samples and data from large mammals is necessary in order to provide accurate scientific documentation about these animals and aid their conservation (Lamb et al., 2016; Solberg et al., 2006). However, there are limitations for science and research: Many projects have a limited budget. This means that the expense of obtaining the samples is limited and needs to be estimated. Some methods to obtain sample material are very accurate, but also very costly (Bellemain et al., 2005). On the other hand, more cost-efficient methods of sample collection have a higher contamination risk or are less accurate (Solberg et al., 2006). Therefore, before sampling, the objectives and hypotheses have to be clearly identified so that the correct methodology can be selected to collect samples and data. In addition, there are other factors in large mammals, such as their high dispersal rates, their frequently decimated populations and their risk to humans, which make data collection challenging (Bellemain et al., 2005; Kindberg et al., 2009). A new rising issue is also the ethics behind the collection of samples and data of wild animals (Arnemo et al., 2006). The goal of an ethic commission is to get data from the large mammals without disturbing or injuring them in their natural environment.

1.3.1 Invasive method

Figure 1. Photograph of a collared Finnish brown bear (*Ursus arctos*) (by Seppo Kemppainen).

In the invasive method, the animals are caught and they get in direct contact with humans (Arnemo et al., 2006; Atwood and Weeks, 2003). From this advantageous situation, it is possible to take some accurate measurements on the animal, such as size measurements and a blood sample, which would otherwise not be possible to take. In addition, individuals can be clearly defined. A further possibility is to equip the animal with a radio collar (Figure 1), which allows scientist to establish movement patterns of the animal and to observe behavioral motives over a longer period of time. The radio collar automatically detaches after a certain time and is collected for reuse. However, before the animal can be captured, it has to be found. In many countries tracking of large carnivores is done with helicopters, as it can cover large areas in a short time (Dahle and Swenson, 2003a). Another option is not to track animals, but to lure brown bears with supplementary food such like a carcass of a moose to a fixed place (Sundell et al., 2006). When capturing, an experienced veterinarian has to be on board, in order to give the animal a short-time anesthesia by a rifle or a blowpipe. Brown bears are anaesthetized with the drug medetomidine-ketamine (Arnemo et al., 2006). During the anesthesia the veterinarian pays attention to the animal's circulatory system, while the radio collar is attached to the animal and hair or tissue samples are taken. But, this method has also some disadvantages: wild animals express stress while getting captured by humans, as they are not used to humans contact. There is a certain even though small risk for those captured animals to die, because of the anesthetic. For the brown bear (*Ursus arctos*), a mortality rate of 0.9% has been calculated between the years of 1984 until 2004 caused by anesthesia (Arnemo et al., 2006). Families, such as a mother and an offspring, can be separated in such an action. In winter, capturing wild animals can consume a lot of vital energy that the animal actually needs to survive. For such methods, an official authorization must always be applied in the project authorization board (ELLA) from the Regional State Administrative Agencies in Finland (ESAVI). The use of the invasive method; need to be well justified due to ethical conflicts, such as unnecessary stress and pain. All these applications from ELLA costs both money and time (Bellemain et al., 2005). In comparison, invasive method has been increasingly superseded by non-invasive methods in recent years, due to some of the benefits discussed in chapter 1.3.2.

1.3.1.1 GIS

Geographic Information System (GIS) is a system for mapping and spatial analysis. Geographically referenced data is stored and associated with non-graphical attributes to process a wide range of information, including manipulation, analysis, modeling and creation of visual maps (University of Maryland, 2012). GIS is widely used in science to qualitatively and quantitatively evaluate regions by their characteristics.

There are several different GIS software, one of them is ArcGIS (University of Maryland, 2012), created by the producer ESRI (Environmental Systems Research Institute). ArcGIS is a collection of various specific analysis areas such as ArcMap or ArcToolbox (Hiller, 2011). The main application is called ArcMap that is used for map display and creation. In this application different spatial relationships can be analyzed. Arc Toolbox, contains tools for geoprocessing, data conversion and coordinate systems. Most data need to be converted to as so called shapefile in order to be used in ArcMap (Hiller, 2011). Shapefile is based on vector data, such as points, lines and polygons to represent map features. A polygon is any 2-dimensional shape formed with straight lines such as triangles or pentagons.

1.3.2 Non-invasive methods

In comparison to the invasive-method, the use of the non-invasive method has increased significantly in the last decades. The term noninvasive is defined as a sampling method where the animals are unaware of sampling and therefore are unaffected by it (Pauli et al., 2010). Certain samples and data may be collected from animals, such as hair or fecal samples left by the animals (Taberlet et al., 1997; Woods et al., 1999), without getting in touch with the animals. Collecting these samples is easy, safe and don´t require special training (Crooks, 2002). The collected samples do not have to be reported and are ready to be used. Thus, enormous costs can be saved (Solberg et al., 2006). Also, the project can be implemented faster, since no large organization and planning in advance is necessary. An important point is also that the animals do not get into stressful situations, since they are never in direct contact with humans. However, the distance involves other risks and disadvantages. Certain samples, such as blood, cannot be collected from the animals. Some issues can only be investigated with the help of blood samples, such as certain diseases. Likewise, it is difficult to determine the size of the home range of an animal, by collecting fecal or hair samples, since the number of the samples are mostly not sufficient enough (Seaman et al., 1999). The data is significantly less accurate, and the error rate increases compared to invasive sampling. There is a chance that individuals cannot be identified from non-invasive samples. The reason for that might be that some samples are too contaminated in order to determine the exact genotype or that genotyping error occurs (Taberlet et al., 1999). For non-invasive sampling it is often required to have several samples from the same individual and the genotypes have to be compared to construct consensus genotype.

1.3.3 Microsatellites

Microsatellites are short non-coding DNA sequences in a living organism. The characteristic of them is that microsatellites are highly repetitive in the genome. Accordingly, microsatellites are also known by the name "Simple Sequence Repeats" (SSR) or "Short tandem repeats" (STRs) (Ellegren, 2004).

The repetitive DNA sequence of the microsatellites often consists of only two to four nucleotides. For each species a specific microsatellite is needed. The locus of a specific microsatellite can vary in the length of the repeats for each individual of a species. Depending on the individual, the respective length of each microsatellite may differ, too. Multiple loci are necessary to identify individuals. The more microsatellites are used, the higher is the probability to detect differences or similarities in individuals. In microsatellite-based studies, length of DNA fragments are compared between the individuals. The more different the alleles of different loci are, the less related the individuals are to one another. On the other hand, two individuals that show similar length in loci are close related. With this method relatedness can be calculated without previous pedigree information (Wang, 2002). An advantage compared to whole genome analysis is that meaningful results can be achieved with significantly lower costs. Also, amplifying only partial regions of the DNA is much easier (Paetkau and Strobeck, 1994). These reasons are why microsatellites have been popular in research and forensics. The method has become so widely used that microsatellite loci of many different species have been identified. In public databases or publications, it is possible to select and to order the necessary microsatellites primers for multiple species from such companies as the Applied Biosystems or Oligomer.

1.4 Study species: the brown bear (*Ursus arctos*)

The brown bear (*Ursus arctos*) is one of the eight bear species existing in the world (Schwartz et al., 2003). They spend most of the time lonely and are thus classified as solitary animals (Sandell, 1989). In comparison with other bear species, it is the most widespread *ursid* (Schwartz et al., 2003). The average body mass of a brown bear is 400 kg, depending on the geographical location and the local food supply (Danilov, 1994). Male bears are on average larger in size and weight more than female bears (Schwartz et al., 2003). One effect of this size polymorphism is that male bears suffer more from disproportional nutrition (Rode et al., 2006) and need bigger food resources. The colour of the fur of brown bears varies from almost yellow to dark brown, depending on the geographical location (Danilov, 1994). During winter, brown bears hibernate from October to March or April (Schwartz et al., 2003).

The mating season is between May and early July (Dahle and Swenson, 2003a). After copulation, 180-266 days of gestation is necessary before cubs are born during the hibernation period in winter, between January and March (Schwartz et al., 2003). Cubs stay with the mother between 1.5 and 2.5 years (McLellan et al.1994), and separate from the mother usually before the mating season starts and the mother gets again into the oestrous cycle (Dahle and Swenson, 2003c). On average 1-3 cubs are born and only the female is responsible of parental care (Figure 2) (Dahle and Swenson, 2003c). Because of the fact that the females take care of the offspring over such a long time, the reproductive rate of brown bears is low and can have strong impact on the population growth rate (Ordiz et al., 2008). The higher rearing effort of female brown bears probably causes, them to be the more selective sex when choosing mating partners (Bellemain et al., 2006b). Brown bears reach sexual maturity at the age of 4-6 years and can grow until they get 10-11 years old. The survival rate is lowest in cubs and increase with the age (Sæther et al., 1998). The oldest wild brown bear has been observed to be over 30 years (Steyaert et al., 2012), but in general they reach an age between 20 and 30 years

Figure 2. Photograph of a female brown bear with two cubs in swamp area in Finland (by Seppo Kemppainen).

Brown bears are Holarctic omnivorous. This means that the diet of the brown bears has a huge variety from plants, such as berries, nuts and grass, till meat, such as moose or salmon (Persson et al., 2001). Bears can be very efficient predators. Depending on time and space, it is possible to observe in brown bears a difference in the food consumption (Steyaert et al., 2013). The further north the home ranges of a bear is, the more meat it consumes (Persson et al., 2001). However, the main food source in the northern Finland does not seem to be reindeer, but moose (Persson et al., 2001). There are two explanations for this phenomenon: i) moose are solitary animals and easier to attack than reindeers and ii) moose are not domestic animals, like reindeers, and are therefore not additionally protected by farmers (Kaczensky et al., 2011). A possible explanation for the higher meat consumption in the north can be that the ground is covered by snow longer in the spring and thus prevents bears from eating insects and berries from the previous autumn.

Even though bears in the north consume more meat, berries are still an important food source in the autumn in order to create a sufficient fat cushion for the hibernation period during the winter (Persson et al., 2001). Besides the large variety in diet, the brown bear occupies a huge variety of landscapes. Brown bears are habitat generalist with wide geographic distribution and can be found in arctic tundra, desert, costal or forest habitats (Figure 3) (Fuller and Kittredge, 1996). The Fennoscandian countries belong to the arctic and boreal ecosystem, characterized by tundra, forest and peatland. For example, 86% of the on Finnish landscape is covered with forest.

1.4.1 Brown bear home range

Despite their predominantly solitary lifestyle, the living areas of brown bears often overlap. Nevertheless, it is possible to identify a certain core area in which the bear stays predominantly over its entire life (Danilov, 1994). In addition, it can be observed that the living area of a male bear is significantly larger than that of a female bear (Dahle and Swenson, 2003a; Schwartz et al., 2003). The behavior and living area of a brown bear do not fit into the definition of a territory. That is one of the reasons, why the term “territory” should be avoided and, instead, name the bear living area as "home range".

The home range of a female bear differs according to the season. Home range is significantly smaller for the bears with an offspring (Bellemain et al., 2006a). At first it was thought that the main reason may be that the offspring cannot move such a long distance. However, Dahle and Swenson (2003a) has shown that the primary reason is probably avoidance of male bears.

Infanticides are quite common in bears. Females try to protect their offspring by trying to avoid contact with male bears by simply reducing their home ranges (Penteriani et al., 2017a). In return, it can be observed that female bears without offspring increase their home ranges compared to the year when they have cubs (Dahle and Swenson, 2003a; Glenn and Miller, 1980).

Like males, also females in estrus tend to roam to mate (Bellemain et al., 2006a). One reason for this is that they are trying to get in contact with several male bears in order to get the best father for the next offspring (Schwartz et al., 2003). By mating with more than one male, the bears also ensure the safety of the future offspring. Bears can recognize one another even after a long time. If the female bear has an offspring and it happens to meet with a male bear with whom it has mated and who can potentially be the father of the offspring, the male will not attack the offspring. For females with small cubs avoiding males is even more important than avoiding human settlements (Rode et al., 2006).

Female brown bears seem to have the tendency not to migrate far from their maternal area (Kojola et al., 2007; Støen et al., 2006). Records of brown bear tracking and observation show that the home ranges of closely related female brown bears overlap with each other (Støen et al., 2005). Similar discoveries were reported also in black bears (*Ursus americanus*) in Canada (Schenk et al., 1998). This, has led to the suggestion that the social interaction of female brown bears increases their individual fitness, possibly due to sharing inclusive benefits such as highly valuable food resources (Griffiths and Armstrong, 2001).

The home ranges of the male bears have different characteristics than the home ranges of female bears. While females are tolerant to human settlements, males try to avoid civilization (Rode et al., 2006). Males have much larger home ranges than females (Schwartz et al., 2003). There are several reasons for this. First, by increasing their home ranges, male bears increase the chance of mating with several females and so on increase their own fitness. This is closely related to the density of the bear population. Males have to increase their home ranges even more in an area of low female density in order to reach high fitness (Støen et al., 2006). Second, male bears are significantly larger than female bears, hence their nutritional cost is higher (Rode et al., 2006).

Male brown bears seem to be more willing to seek for new regions and mating partners after they have become sexually mature at the age of ~ 3-5 years old (Støen et al., 2005). Subadult male brown bears migrate to new areas and create there their own home range (Glenn and

Miller, 1980). The reason for the dispersal behavior of subadult bears is that by moving into new areas, more distant from their birth place, male brown bears avoid inbreeding (McLellan and Hovey, 2001; Støen et al., 2006). The chance of meeting related brown bears is significantly less the further the bear is from its natal area. Also, subadult male brown bears are not territorially accepted by older males in their areas (Støen et al., 2006). It has been reported that those subadult male brown bears settle their home range closer to human places and resorts (Nellemann et al., 2007).

1.4.2 Brown bear distribution

The distribution of the brown bear is mainly focused on the northern hemisphere, as it can be seen in Figure 3. The total number of the brown bears was estimated to be 200.000 individuals in the IUCN list (Ria et al., 2016). This is just an approximate population size estimate, as the census population size has never been reliably estimated. Just in few places in North America and Europe the population size (Bellemain et al., 2005) and spatial structure (Manel et al., 2004) of brown bears have been estimated more accurately. The largest number of brown bears is existing in Russia. Hunting is still allowed in Russia and there is no legislation for protecting the bear population. Nevertheless, it seems that the population size is stable (Kojola and Heikkinen, 2006). Russian brown bear population can be seen as a source population for brown bears in Finland (Kopatz et al., 2014), as the Finnish brown bear population suffered a strong decline in the beginning of the 20th century. After the 20th century the brown bear population was able to recover and to increase the population size again, with the help of immigrating brown bears from the Russian side (Kojola etal., 2007). The migration between Russia and Finland protected the population from a strong bottleneck effect and had also kept the genetic diversity high.

The brown bear population was historically distributed along the whole Europe, but because of intensive habitat destruction and overexploitation, the bear population has dramatically declined (Kojola and Heikkinen, 2006). Brown bears are extirpated from some countries, such as Germany, the Netherlands and Denmark (Zedrosser et al., 2001). Nowadays 22 European countries have brown bear population and the total number of brown bears in Europe is about 50 000 individuals (Zedrosser et al., 2001). In the 21st century, countries such as Sweden, Norway and Finland have reported a great reintroduction of large carnivores (Clark et al., 2002). It seems that brown bears were able to re-establish a stable population to these countries during the last 50 years, unlike in other parts of the Europe. Small scattered populations can be found isolated in Spain, France, Italy and Greece (Kaczensky and Chapron, 2012). Dividing bears into subpopulations a total number of 10 subpopulations have been identified in Europe (Kaczensky and Chapron, 2012).

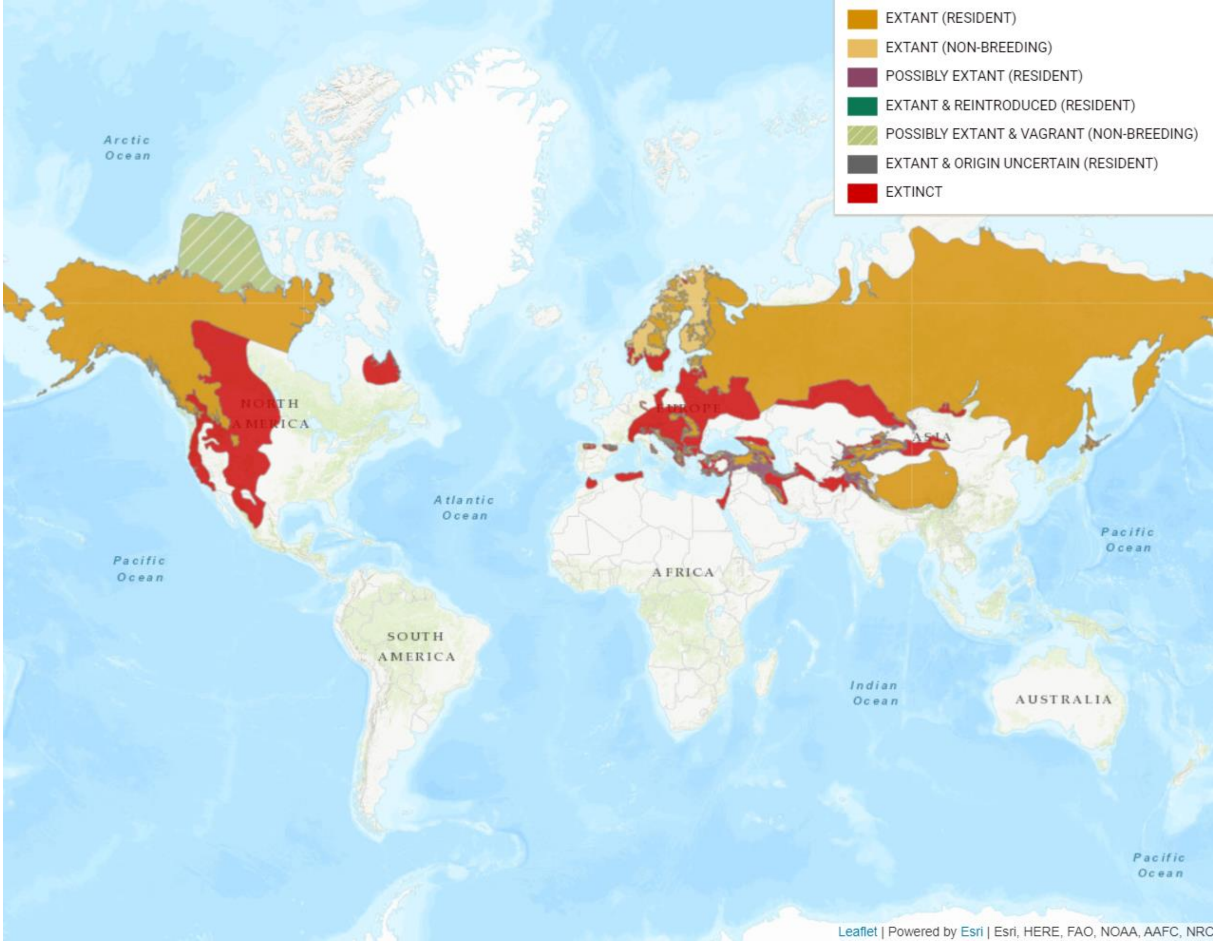


Figure 3. Geographic distribution of brown bear (*Ursus arctos*). Distribution data is from the IUCN red list of threatened species (Version 2019.2).

The current distribution of brown bears in Finland is unequal. A high density can be found on the east side of Finland close to the Russian border (Figure 4) (Saarma and Kojola, 2007). In Central Finland the density is significantly reduced, nevertheless it is possible to find a regular occurrence of brown bears. For this reason, two constantly present populations in Finland exist: Eastern Finland and Central Finland. The Eastern Finland brown bear population was the only brown bear population that survived the strong exploitation in the past. This was achieved by the connectivity to the Russian Karelian population (Kojola et al., 2007). Constant migration from the Karelian brown bear population kept the population stable and less related in Eastern Finland (Kopatz et al., 2014). After the strict protection in the 20th century of brown bears in Finland, the population were able to expand back also to other parts of Finland (Kojola and Heikkinen, 2006). In particular Central Finland observe a successful return of brown bears and a stable population has been established (Figure 5). In contrast to that, the return in Northern Finland is runs difficult. This is due to reindeer husbandry and a higher amount of bear poaching in the north (Swenson et al., 1997)The current population size of brown bears in Finland is between 2020–2130 individuals (Heikkinen et al., 2018). The census size estimate of the brown bear population in Finland is published each year between February and April by the natural resources institute of Finland (Luke). The census size is estimated from the previous year's bear litter observations (Table 2) (Heikkinen et al., 2018).

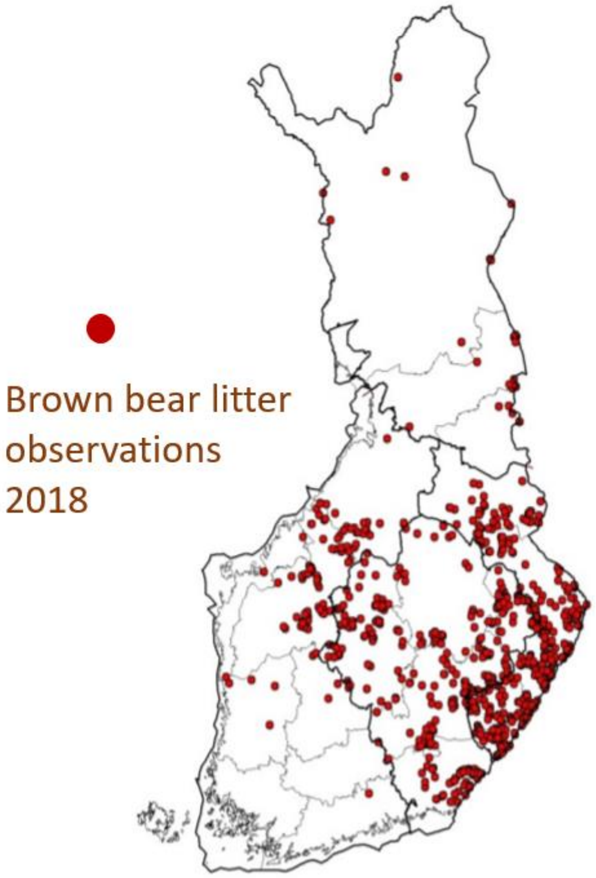


Figure 4. Geographic distribution of the litter observation of brown bear (*Ursus arctos*) in Finland in the year 2018. Brown spots are the individual bears (Total n = 948) (Heikkinen et al. 2018).

Table 2. Adult and litter observations of brown bears in Finland from 2013–2018.

	2013	2014	2015	2016	2017	2018
Adult bear observations	11 193	10 359	11 426	12 398	13 477	10 144
Litter observations	794 (7.1 %)	1 216 (11.7 %)	1 224 (10.7 %)	1 194 (9.6 %)	1 639 (12.2 %)	948 (9.6 %)

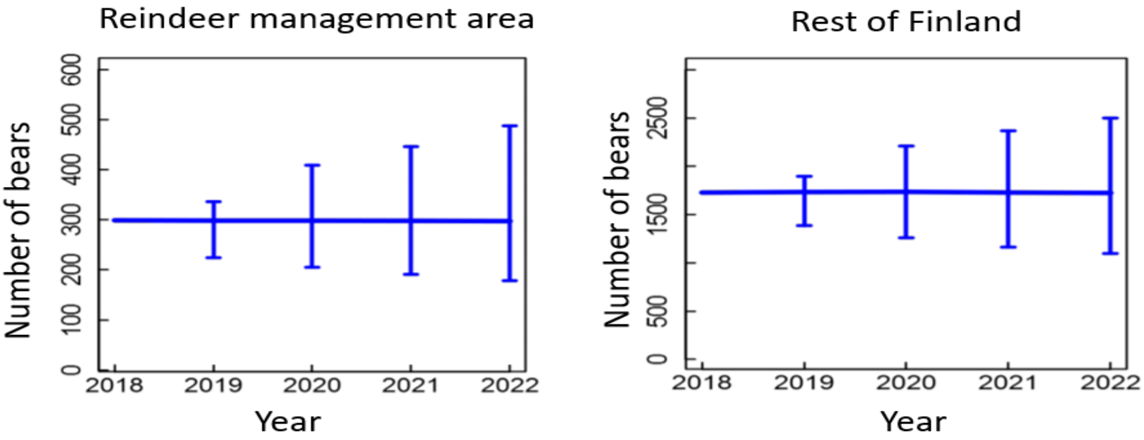


Figure 5. Prediction for the brown bear population size for 2018-2022 with a known mortality of 14%. The bars indicate the upper and lower limits of the 95% interval (probability distribution). Reindeer herding area (left) and elsewhere in Finland (right). Data collected by Luke (Natural resources Institute Finland) (Heikkinen et al., 2018).

1.4.3 Threats and conservation actions for brown bears

Nowadays bears have to deal with several threats around the world (Swenson et al., 2000). Some threats are focused just on specific areas, but most of them are common anywhere where brown bears can be found. One major threat is the habitat loss and habitat fragmentation of the living areas of the brown bears (Crooks, 2002; Kaczensky et al., 2003; Waller and Servheen, 2005). With the constantly increasing human population more space is needed for food production such as agricultural fields, increased forestry or human settlement (Nellemann et al., 2007; Zedrosser et al., 2001). Along with the habitat destruction also the climate change can cause some threats on brown bears. With the global warming the amount of pathogenic diseases may increase in Finland. Permafrost is thawing and opening more peatlands. Plants adapted to the subarctic conditions suffer more interspecific competition, so that the food web might change for brown bears (Costello et al., 2014). Same as in the past, trophy hunting and protection of the livestock such as reindeers from brown bears (Figure 6) is still common same as for other large carnivores such as wolves (Kojola et al., 2006). Legal hunting was in the past a major threat for large carnivores (Figure 7) (Cederlund and Bergström, 1996; Kaczensky et al., 2011). Nowadays the bear is strictly protected and its hunting is regulated by the Habitats Directive of the European Union. Illegal poaching is forbidden by the government and is punished strictly. Furthermore, it is socially not accepted. Damages in the livestock caused by brown bears are compensated either by the state, regional government or hunter clubs (Zedrosser et al., 2001).

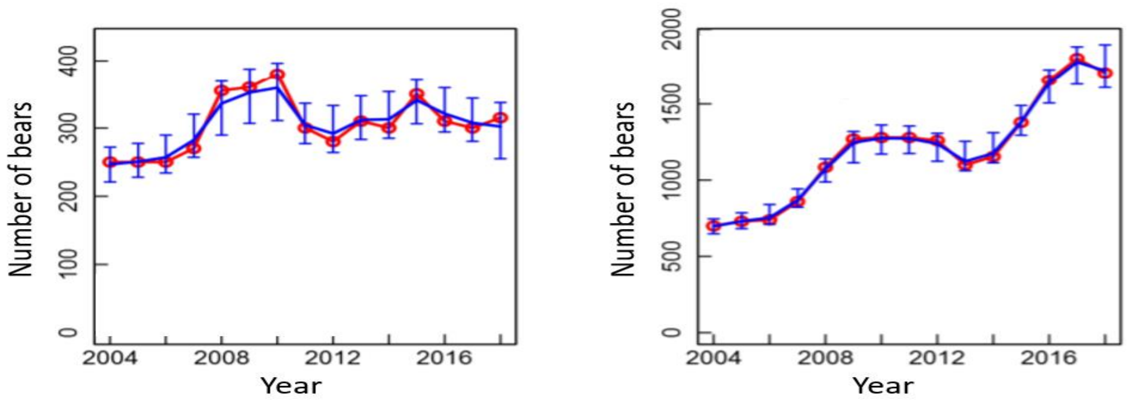


Figure 6. Bear population development from 2004 until 2018 in the reindeer herding area (left) and elsewhere in Finland (right) (Heikkinen et al., 2018).

Finnish bear population has reached a stable population size again and hunting permits have been given, as the defined official population management plan. Bear hunting season starts on the 20th of August each year (Heikkinen et al., 2018). In order to be able to hunt bears a hunter has to pass a hunting exam. The hunting quota is set by the Finnish Ministry of Agriculture and Forestry. Finnish Wildlife Agency´s mandate for grant exceptional permits are limited and need to be reasonable (Figure 7). Bear kills have to be reported immediately to the Finnish Wildlife Agency and the police on the first weekday after the kill.

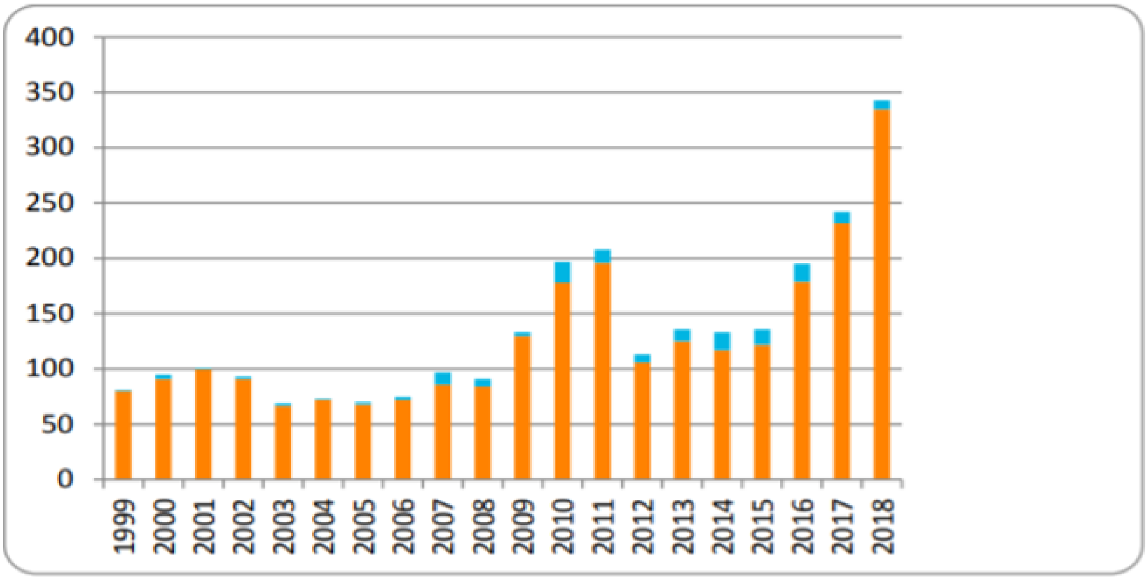


Figure 7. Known bear mortality. Bear mortality in Finland caused by hunting is marked with orange bars. Other causes for bear mortality are shown with blue bars (Heikkinen et al., 2018).

1.5 Aim of the study

All the strict regulations of the brown bear have one goal: the protection and conservation of the brown bear population in Finland. A great knowledge of the species is necessary for the success of wildlife management plans. Knowledge is often based on recent scientific studies and regular estimation on population census size (Luke). With the help of genetic analyzes, the population structures of brown bears in Finland have been successfully analyzed (Hagen, 2015; Kopatz et al., 2012). Migration processes and the link among the brown bear populations in Finland, the Scandinavian country and west part of Russian have been demonstrated (Kojola and Heikkinen, 2006; Kopatz et al., 2014). However, knowledge about the social structures among brown bears in Finland is only suspected on the basis on publications from abroad (McLellan and Hovey, 2001) or of other bear species (Schenk et al., 1998). In Sweden, researchers have found out that the home ranges of bears overlap in various degrees (Støen et al., 2005). It seems that there is social structure among the bears. This is a contradiction to some publications that portray the brown bear as a non-social animal (Bellemain et al., 2006a). The aim of this master's thesis is to determine the social structures of the brown bears in Finland, asking the question: "Who shares their home ranges with whom?". Due to the historical unequal distribution of the brown bear population in Finland, two different characteristics can be observed in the brown bear population: i) Brown bear population in Eastern Finland has a high population density and is subject to constant migration from Russia. ii) Brown bear population in Central Finland has a low population density and consists of the expanded Eastern Finland population. For this purpose, genetic analysis with microsatellite data and radio collar data stored in ArcGIS were used to determine the home ranges and relationships between the studied bears.

Three hypotheses have been set up:

1. In Central Finland brown bears are closer related than brown bears living in Eastern Finland.
2. In Eastern Finland brown bear home ranges are in average smaller, than home ranges in Central Finland.
3. A positive correlation exists between the relatedness and overlap of home ranges.

2. Material and Methods

2.1 Study area

The study area was mainly focused on the Eastern and Central part of Finland (Figure 8) as most brown bears occurs in those two parts. All bears were mostly in Finland during the time of tracking and were just shortly crossing the border to Russian. The studied area in eastern Finland covers the following municipalities: Juuka, Valtimo, Ilomantsi, and Lieksa, and the study area of central Finland: Keuruu, Petäjävesi, Orivesi Alajärvi, Saarijärvi and Kyyjärvi. In the Eastern part of Finland close to the border with Russia (Karelia), the area consists of a wide forest zone, which can range in width from several hundred meters to several tens of kilometers. No human activity is allowed in this area, which gives this area the characteristics of a large nature reserve. Also the fauna is significantly more diverse in the eastern part of Finland than in the rest of the country (Saarma and Kojola, 2007). Central Finland is characterized by the boundary between two vegetations zones, On the one hand the northern zone with species like the Alpine Catchfly (*Lychnis alpine*) and the southern zone with species like the German Catchfly (*Lychnis viscaria*). The soil in this area is rugged and does not have many nutrients the dominant species are non-demanding forest and mire vegetation. Along villages and lakes, patches with humid microclimate of old growth forest exist. In the past forestry was the main income for the settled humans in Central Finland. In non-protected areas forestry is still present and young forest dominate (Metsähallitus, 2020).

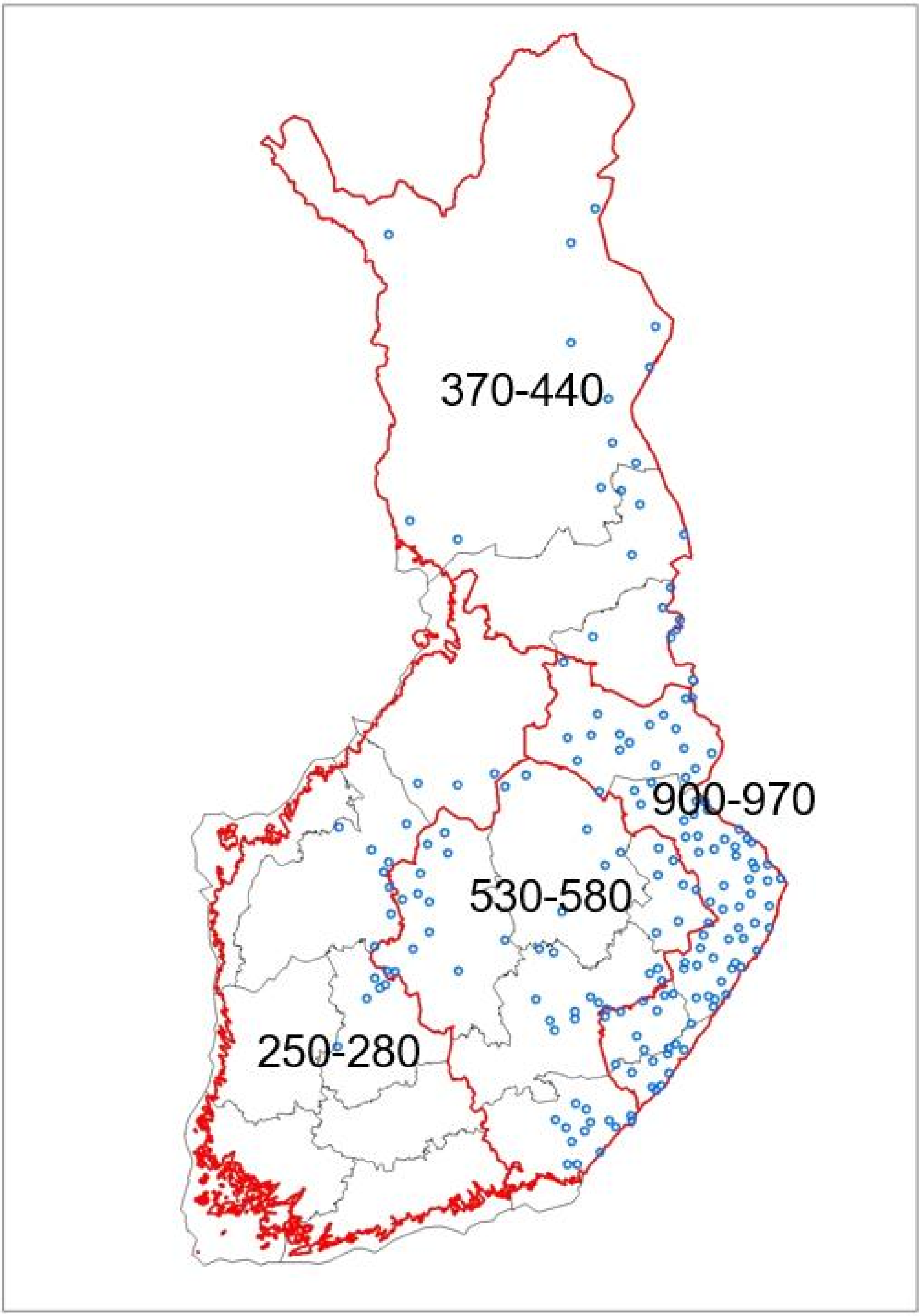


Figure 8: Map of brown bear (*Ursus arctos)* distribution in Finland. Amount of brown bears for each district. Created by Ilpo Kojola 2010 PP.

2.2 Sampling

A total of 119 bear samples were analyzed in this study. During the collaring procedure of GPS tracking items on the bears between the years 2004 and 2014, 53 bear samples were collected. The other 66 samples have been collected during the hunting season from volunteers, mostly hunters, in the years 2000 and 2014. The collected samples were sent to the University of Oulu for further investigations. Genetic analyses were done in the laboratories of Ecology and Genetics Research Unit in the university of Oulu during the years 2017 and 2019. The samples consisted of either saliva, hair or tissue samples of trapped bears.

2.3 Laboratory analysis

2.3.1 DNA Extraction

For the DNA extraction from bear saliva and skin the DNA Isolation Kit MoBio Ultra Clean® was used. According to the manual of MoBio Ultra Clean® the extraction process of the DNA and were stored in a box in a freezer. The procedure of extraction was mostly following the manual of the manufacturer and just small changes were done in the working protocol, as it promised to be even more successful in the extraction of brown bear samples. The extraction of the DNA took place in a semi-clean laboratory, which is sterilized with UV light for 30 minutes after each use.

For the DNA extraction of the hair samples the DNA Isolation Kit E.Z.N.A® Tissue DNA was used. The DNA was extracted according to the manual of the extraction kit and samples were stored the same way as tissue.

In order to be sure whether enough DNA was extracted from the hair or tissue sample, the concentration of the DNA in the extract were measured using the Thermo Scientific NanoDrop spectrophotometer. The Nanodrop only needs a small amount of extract material (approx. 1-2µl) to make quantitative estimate of the DNA concentration. 1µl from the extract were pipetted to the measuring device. In the measurement, light is sent through the sample liquid and compared with the reference value (distilled water). The closer the value is to zero, the lower DNA concentration is available.

2.3.2 Microsatellite genotyping

The extracted DNA, was amplified in a polymerase chain reaction (PCR) using 11 bear primers. The reaction mixture for the PCR analyses is shown in Table 5, and the thermal cycling program in the PCR for the DNA-amplification is shown in Table 4. Primers were ordered from the company Applied Biosystems and stored in the freezer. All 11 primers have been used in numerous bear publications. The first time primers G1D, G10B, G1A and G10L were used was with the black bear publication by (Paetkau and Strobeck, 1994) and the polar bear publication by (Paetkau et al., 1995). Primers MU05, MU09, MU10, MU50, MU51, MU59, MU15 were developed in (Taberlet et al., 1997). The primers have been already successfully used for Finnish brown bears studies by (Kopatz et al., 2012, 2013, 2014) at the university of Oulu .The primers were divided into 4 groups so that the allele sizes in one primer group don't overlap with each other (Table 3).

Table 3. Multiplex Primer groups: With name, Coding region and Fluorescent marker.

Group 1	*Group 2*	*Group 3*	*Group 4*
MU09 (101-129) PET	MU05 (112-134) PET	G10B (98-122) NED	MU50 (105-129) FAM
MU15 (107-119) VIC	G1OL (165-192) NED	MU51 (125-150) FAM	MU10 (130-148) VIC
G1D (160-210) NED	MU59 (210-260) FAM	G1A (175-200) PET	

Table 4. Thermal cycling program used in the amplification of the samples with 11 primers divided in 4 multiplex primer groups.

Step	*Number of cycles*	*Temperature*	*Time*
Pre-incubation	1	95°C	15min
Denaturation		94°C	30sec
Annealing	35	60°C	90sec
Elongation		72°C	30sec
Final Elongation	1	72°C	5min
End	1	4°C	∞

Table 5. Reaction mixture for multiplex PCR amplifications using a group of 3 primers.

Component	*Volume 1 Sample*
Master mix (Qiagen Multiplex PCR Kit)	5µl
Primer mix F + R (10µM)	0,2µl (each Primer) x 3
H2O	2,4µl
DNA	2µl
Total Volume	**10µl**

To check weather each PCR run was successful an agarose gel electrophoresis was carried out. The gel electrophoresis consist of an 80 µl agarose gel with a buffer solution containing a mixture of tris base, boric acid and EDTA (TBE) and 3 µl Midori Green. The gel consists in one side of the gel with wells. The first and last wells is filled with 1 µl Ladder (100 bp Plus DNA 0,5 µg/µl,50 µg), 1 µl Loading buffer and 2 µl H2O. All other wells contain of 3 µl DNA products from the PCR and 1 µl Loading. The DNA samples are loaded from 96-well plates in the wells of the agarose gel. An electric field is connected to the agarose gel with 110 V over 60 minutes. DNA fragments are negatively charged which means that the DNA fragments move towards the positive electrode. Small DNA fragments move through the gel faster than large ones. After 60 minutes the gel can be removed from the electric current and the different DNA fragments can be seen and analyzed with a gel screening device.

Gel Doc EZ System is a device in combination with the Image Lab software that enables DNA fragments to be visualized in form of fluorescence images after gel electrophoresis. Gel Doc detect the Midori Green staining with UV sensors, which was add to the sample with the DNA. The DNA fragments can be seen in the software as gray bands. If there are no bands, there are no DNA fragments in the gel electrophoresis. This method has several advantages over other gel electrophoresis imaging method: i) The application is quick and easy. The analysis can be completed in a few minutes after switching on the device. ii) Furthermore, the Gel Doc EZ system creates and saves high-quality images that enable further precise analyzes. The device is not only able to recognize Midori Green in the sample, but it can also detect other substances, such as copper, silver and zinc.

In order to obtain the exact sequence information from the amplified DNA, the DNA samples were finally analyzed in the capillary electrophoresis genetic analyzer (ABI PRISM 3730 DNA Analyzer). The ABI genetic analyzer works according to the following principle: The individual DNA fragments are marked with fluorescent dye. Depending on the size of the amplified DNA, several fluorescent dyes can be detected in one sample. Depending on the fluorescence intensity, the size of a DNA fragment is calculated and displayed in the form of a standard curve.

Based on the results from the ABI genetic analyzer the exact fragment size can be examined by using the Genemapper software (GeneMapper® software, version 4.0 Applied Biosystems © 1999-2005). This software can determine the fragment sizes of different individual loci by comparing the fragment size to sizing curve, which has been created by the GeneMapper. All lengths in one locus and between different loci varies in length. The results are summarized in an excel table for the further evaluation of the loci in a population. Loci that did not have a clear size curve in a sample were marked as missing data.

2.3.3 Genotyping error

A genotyping error occurs when an individual's amplified genotype does not match to the true genotype (Pompanon et al., 2005). The analysis of genotyping errors is important in order to determine the veracity of a result. Genotyping errors often occur on markers, such as Single-nucleotide polymorphism (SNPs) and microsatellites, which are used for the genetic analysis of population structures (Pompanon et al., 2005).

There are several causes that can lead to a genotyping error. Basically, it can be assumed that with an increased amount of data, the risk of errors increases: 1. There may be interactions between DNA molecules, such as a mutation in the target sequence of a primer. As a result, no allele is detected. 2. With low quality and quantity of the DNA sample or contamination of the DNA extract, the probability of a genotype error increases as well. This can lead to allele scoring mistake. 3 Another cause for genotyping error are biochemical artefacts on devices, such as a Taq polymerase error during PCR. (Pompanon et al., 2005) 4. In addition, human errors such as incorrect sample labeling or a misinterpretation can occur in data processing which can lead to a genotype error (Bonin et al., 2004).

Most common way to determine genotypes error is based on the assumption of the mendelian inheritance. The per-reaction error rate (el) per locus (l) can be estimated as follows:

(1)

$$e_l \approx \frac{1}{2P_l} \cdot \frac{m_l}{M_l}$$

With number of mother-offspring mismatches (ml), number of mother-offspring pairs (Ml) and the exclusion probability at that locus (Pl) (Hoffman and Amos, 2004). A genotyping error can be determined by comparing known mother-offspring pairs by searching for mismatches (Hoffman and Amos, 2004).

Genotyping errors should not be neglected in a study, as it can have some far-reaching consequences for the evaluation of population structures, such as: incorrect allele frequencies, incorrect F_{ST} estimates, incorrect recognition of the selection of the population bottleneck. When calculating the population size and genetic identification of individuals, the actual population may be incorrectly overestimated (Bonin et al., 2004).

In order to reduce the genotyping error during the analysis, certain procedures are recommended: Positive and negative controls should be used for genetic analyzes and it is advisable to evaluate the DNA samples independently several times. (Hoffman and Amos, 2004). Replicates that were created by another technical device can also be recommended. In conclusion, the procedures in the laboratory should be well known (Bonin et al., 2004).

2.4 Genotype data analysis

2.4.2 Genetic diversity

In order to estimate the genetic variation of a population, several values are important. One of those estimates is allelic richness. It was estimated the software FSTAT and it evaluates the genetic diversity of each population in terms of allele numbers (Foulley and Ollivier, 2006; Greenbaum et al., 2014). With this value it is possible to predict the potential of adaptability of a population to different environments and persistence in the future (Greenbaum et al., 2014). The inbreeding coefficient (F_{IS}) was calculated by the software GENEPOP. The F_{IS}-value describe the reduction in heterozygosity of an individual due to non-random mating within its subpopulation within one generation. There are different ways of determining the F_{IS} value in a population. With GENEPOP it is possible to estimate F_{IS} using the Weir and Cockerham (1984) equation as well as the Robertson and Hill equation (1984). In this study, the value from the Weir and Cockerham equation, since it is better suited to small population sizes (Weir and Cockerham, 1984). Observed and expected heterozygosity has been calculated by the software GenAIEx 6.5 (Peakall and Smouse, 2006). GenAIEx 6.5 stands for the abbreviation Genetic Analysis in Excel and it estimates the proportion of a population that is heterozygote for at least one of the studied loci (Nei, 1978). The observed heterozygosity evaluates how many individuals are heterozygous. The expected heterozygosity evaluates the number of different alleles for each locus assuming the Hardy-Weinberg equilibrium. Also, probably of identity (P_{ID}) can be estimated using the software GenAIex. It determines whether the number of loci (11), is sufficient to identify individuals reliably and to obtain meaningful results in relation to the degree of relatedness. Principal component analysis (PCA) was done, using the software GenAIEx. PCA is an algorithm to transform the columns of a dataset into a new set of features called principal components. The advantage of principal components is to find strong patterns from a large and complex dataset. In this case it is used to determine, if the different locations (Central and Eastern Finland) genetically diverged from each other in brown bears.

As a final step for the Finnish brown bear population structure Geneplot was created. With this approach (McMillan and Fewster, 2017), it is possible to visualize the distribution of populations according to their genotype probability. For the visualization quantile lines out of the genetic information were calculated and compared among the two populations

2.4.2 Kinship estimation

For the kinship estimation, the larger sample of bears was increased to 118 in order to achieve more accurate allele frequencies in the population. The data for the relatedness analysis consisted of 53 brown bears, which were marked and tracked with the help of GPS collars. In addition, there were another 65 brown bears, that were living in the study areas but have not been equipped with a GPS collars.

There are different software how to examine genetic samples. Not every software is suitable for analyzing certain da ta and each case has to be tailored to the sample material and to the research question (Taylor, 2015; Waits et al., 2001; Wang, 2014). Relatedness can be estimated from microsatellite genotypes that often may include null alleles. If null alleles are detected but analysis are not adjusted accordingly, it could lead that the relatedness and thereby relationships between individuals can be estimated incorrectly. That`s why it is important to choose a correct software for estimating the relatedness that takes null alleles into account (Wagner et al., 2006).

For this study the software ML-Relate software (Kalinowski et al., 2006) was chosen as with the help of this software it is possible to determine the maximum likelihood of relatedness and relationships. This is done in ML-Relate by using genetic information, in this case, microsatellites. Relatedness (*r*) are mathematically represented probabilities (*k*) in which the individual shares the genotype (zero, one or two alleles in a locus) with other individuals by being identical by descent. Furthermore, the program assumes that no inbreeding took place in that population and that it is a closed population.

Mathematically represented, the relationship between the k coefficient and the relationship coefficient (*r*) is as follows:

$$r = \frac{1}{2}k_1 + k_2. \tag{2}$$

Parent-offspring k_0=1, k_1=0, k_2=0; Full-siblings k_0=0.25, k_1=0.5, k_2=0.25. If inbreeding needs to be included, additional coefficients in the equation are necessary (Kalinowski et al., 2006).

The relationship between two individuals from the genetic data can be represented by k-space or from the vector K = (k_0, k_1, k_2). The maximum probability of r is estimated between two individuals by searching the entire parameter space of K and finding the highest K-value.

Afterwards a statistical analysis of the program is performed, which assesses the uncertainty in the estimate of relatedness.

(3)

$$\Lambda = \text{Ln}\left[\frac{L(\mathbf{K}_{Putative})}{L(\mathbf{K}_{Alternative})}\right].$$

The simulation assumes that the allele frequencies in the population are equal to the allele frequencies in the sample. Genotypes are simulated in two steps. First, the number of alleles identical by descant is chosen from K and then genotypes are chosen given by the value K. If P value is smaller than 0.05 the alternative hypothesis is rejected.

The program has three main advantages: 1. The program is freely available on the web and is compatible with Microsoft Windows. 2. It calculates kinship relationships based on maximum probability calculations. In comparison with other calculations for family relationships, it has been found that it has a lower root mean squared error (Milligan, 2003). 3. Null alleles can also be included in this program.

The t-test is a statistical tool that determine the probability that the means of two sets of data are different. In this study, the goal of the t-test was to determine if the brown bear population differ in their degree of relatedness between Central and Eastern Finland and between male and female brown bears. Both data need to be normally distributed (Razali and Wah, 2011). In order to calculate a t-test, it is necessary to calculate the difference between the mean values from each data set (mean difference), the standard deviation of each group and the number of data values of each group. There are several different methods of t-tests, depending on the hypothesis that need to be tested. In the two-tailed t-test the data is tested whether a sample is greater than or less than a certain range of value and were used for the comparison of the relatedness of brown bears in Eastern and Central Finland. The two tailed t-test was calculated by the software R-Studio.

2.5. Spatial analysis

2.5.1 Estimation of home ranges

For the estimation of home ranges, the software ArcGIS (Geographic Information System) were used as it is widely known in science to qualitatively and quantitatively evaluate geographic areas. The newest ArcGIS version 10.7.1 is available at the University of Oulu and can be used free of charge by students and staff.

GPS coordinates for the bear population in Finland were collected between 2004 and 2014. 53-radio collared brown bears, there were regularly collected data available from 39 individuals, including GPS locations and timepoints. From the remaining 14 bears, mostly males, there were insufficient or no data available. These bear individuals were excluded from further analysis.

From the collected data, GPS locations and time points were extracted for each individual bear into excel table. The next step was to exclude the period in which the bears are in hibernation, as they could otherwise falsify the kernel home range calculation. Only the months from May to September were used in the calculation of the home ranges. All excel tables were combined into a shapefile and adapted to the coordinate system EUREF_FIN. The layer consisting the map of Finland was also created by ArcGIS using the same coordinate system. Additionally, for the analysis of home ranges of each bear individuals, the extension HRT (Home range Tools) was installed in AcGIS. It was developed to study movement backgrounds from animal habitats in more detail (Rodgers and Carr, 1998).

In this study, the home ranges were calculated with the help of kernel home ranges estimates, since kernel estimations have already achieved great success in other data home range analyzes (Laver and Kelly, 2008; Seaman et al., 1999). Kernel estimates are not parametric, which means that they are not based on the data that correspond to a specified distribution parameter (Seaman et al., 1999). Kernel home range estimations are estimating probability densities from a set of points (Rodgers and Carr, 1998). For an accurate home range analysis, it is not only important to select the most accurate method, but also to have a certain minimum amount of datapoints. The more data available, the more accurate is the home range calculation. If the sample size is too small, the actual home range could be underestimated (Seaman et al., 1999). The paper Seaman 1999 recommends a sample size of at least 50 datapoints per home range calculation. In total an amount of 83414 GPS data has been successful analyzed. Removing one sampling year of one bear individual that contained just 8 GPS locations, an average of 897 GPS locations per Home range for each year and bear individual were calculated. For each individual and years 80%, 90% and 95% kernels were calculated with the software home range tool (HRT). Kernel of the home range is the core area of a bear's living area. Extreme values of the collected data can be excluded by specifying the percentage of the available data that should be analyzed. Using all the collected data could lead to an overestimation of the bear's home range. In this study a percentage of 80% -95% of data were analyzed. This is a sufficient amount to create a realistic home ranges as only the extreme values were removed (Seaman et al., 1999). The calculated home range kernels are presented in ArcGIS as a donut polygon.

The t-test can only be used if the data follow a normal distribution or a Gaussian distribution (Razali and Wah, 2011), but this is not always the case in this study. In some data, the distribution of the results can be recognized visually with the help of graphs. But if a normal distribution cannot be recognized graphically or it is too imprecise, a distribution test can be used in order to determine the normal distribution. The Shapiro-Wilcox test (Shapiro and Wilk, 1965) were chosen in order to determine the normal distribution. The prerequisite for the Shapiro-Wilcox test is that the sample size cannot be larger than n = 5000 and not smaller than n = 3. Furthermore, the samples must be independent from each other. The advantage of the Shapiro-Wilcox test to other tests such like the Kolmogorov-Smirnov test, is that this test can detect deviations from normal distribution even from a small amount of data (Razali and Wah, 2011). The Shapiro Wilk test is composed of the formula:

$$W=\frac{b^2}{(n-1)s^2} \tag{4}$$

With b^2 as the expected variance and s^2 as the sample variance. The two Wilcox-Shapiro Test was calculated by the software R-Studio. In this study, the Shapiro-Wilk test were used to determine whether the home range size is normal distributed. If the value is under the significant value of 5% the home range size is not normally distributed and the statistical analyze has to be different in comparison to statistical analyses of the degree of relatedness of brown bears. The Mann-Whitney-U-Test compares the median between two independent groups that are not normal distributed (Nachar, 2008). Nonparametric test has to be used, if the data is not normally distributed based on for example Shapiro-Wilk test. The Mann-

Whitney-U-test is a nonparametric test for independent variables. The Mann-Whitney-U-Test is composed of the formula:

(5)

$$U = \min(U_1, U_2)$$

Where:

$$U_1 = n_1 n_2 + \frac{n_1(n_1 + 1)}{2} - R_1$$

$$U_2 = n_1 n_2 + \frac{n_2(n_2 + 1)}{2} - R_2$$

with n_l and n_2 as the sample size and R1 and R2 as the sum of the ranks. The two Wilcox-Shapiro Test was calculated by the software R-Studio. The Wilcox Shapiro Test were used in order to determine whether the size of the home ranges differ between the brown bear population in Central and Eastern Finland, between female and male brown bear and between female with cubs and without cubs.

2.5.2 Home range overlap

To calculate the overlap of the home ranges between individuals, all polygons were reassembled in a new shapefile and uploaded to ArcGIS. Each attribute (year and individual) was individually tested for overlap with other individuals. Since the new shapefile is made out of many different layers, it must reformat using the Multipart to Singlepart tool, so that there is only one layer available with all the data. With the UNION tool, all overlaps of home ranges (90% kernel) of bears were determined for each year. All bears that showed no overlap in the specific year of the home range kernels were removed with the Delete Features Tool. From the overlapping home ranges, the overlapping area (m^2) were calculated with the Summary Statistics tool.

Finally, all calculated home ranges and overlaps were transferred in an excel file. The percentage of overlapping home ranges (HR) between two bear individuals (A_i ; A_j) were calculated with the formula:

(6)

$$HR = \frac{O_{ij}}{(A_i + A_j)} \times 2$$

where O_{ij} as the area of overlap between bear i and bear j, and A_i and A_j as the areas of the home range between the month May until September of bear i and bear j (Atwood and Weeks, 2003; Ratnayeke et al., 2002; Støen et al., 2005).

2.6 Home range overlap and the relatedness of brown bears

Correlation between the relatedness and the home range overlap among female and male bears were estimated using the Spearman correlation, which measures the relationship between two variables. In comparison to the Pearson Correlation, the Spearman correlation measures the monotonic relationship, while the Pearson correlation measures the linear relationship. Most of radio-collar data are non-parametric which is the reason Spearman correlation is often used in this type of studies (Ratnayeke et al., 2002; Støen et al., 2005). The difference in the equation is that the Spearman correlation does not calculate the data points themselves, but between their ranks:

(7)

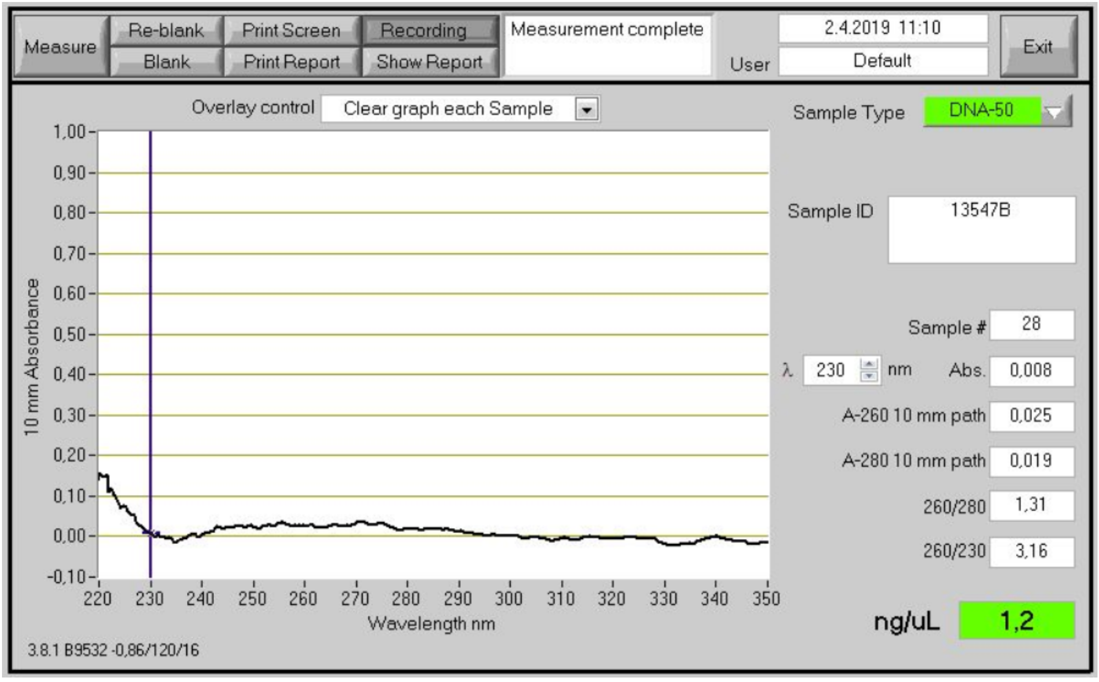
$$\rho = \frac{S_{xy}}{S_x S_y} = \frac{\frac{1}{n}\sum_{i=1}^{n}\left(R(x_i) - \overline{R(x)}\right)\cdot\left(R(y_i) - \overline{R(y)}\right)}{\sqrt{\left(\frac{1}{n}\sum_{i=1}^{n}\left(R(x_i) - \overline{R(x)}\right)^2\right)\cdot\left(\frac{1}{n}\sum_{i=1}^{n}\left(R(y_i) - \overline{R(y)}\right)^2\right)}}$$

With R(x) and R(y) are the ranks and R(x)bar and R(y)bar are the mean ranks. Spearman correlation between the relatedness of the bear individuals and the home range overlap and among female and male bear individuals were calculated by the software R-Studio with the package (Harrell, 2019).

3 Results

3.1 Amplification of microsatellites

DNA of 53 hair or tissue samples were extracted and the DNA content was measured using Nanodrop (Figure 9). In average the measured concentration of the extracted DNA samples was at the wavelength of 230 nm around 13 ng/uL. This value was on the one hand enough in order to be able to continue with the amplification of microsatellites and on the other hand low that samples did not need to be diluted.



Measurement complete

2.4.2019 11:10

User Default

Overlay control Clear graph each Sample

Sample Type DNA-50

Sample ID 13547B

Sample # 28

λ 230 nm Abs. 0,008

A-260 10 mm path 0,025

A-280 10 mm path 0,019

260/280 1,31

260/230 3,16

ng/uL 1,2

Figure 9. An example of a Nanodrop measurement of an DNA-extraction. Measurement of the DNA-concentration was set for all samples at the wavelength 230nm with distilled water as the zero reference. Sample ID 13547B.

All 53 samples had sufficient DNA concentration for microsatellite amplification. The amplification success was examined using gel electrophoresis (Figure 10). A negative control was always added in order to check for exogenous DNA contamination (Bellemain and Taberlet, 2004). A positive control was not anymore included in an electrophoresis, since all

11 microsatellites has been used already and has been successfully tested on bear samples under the same conditions in the same laboratory (Kopatz et al., 2012).

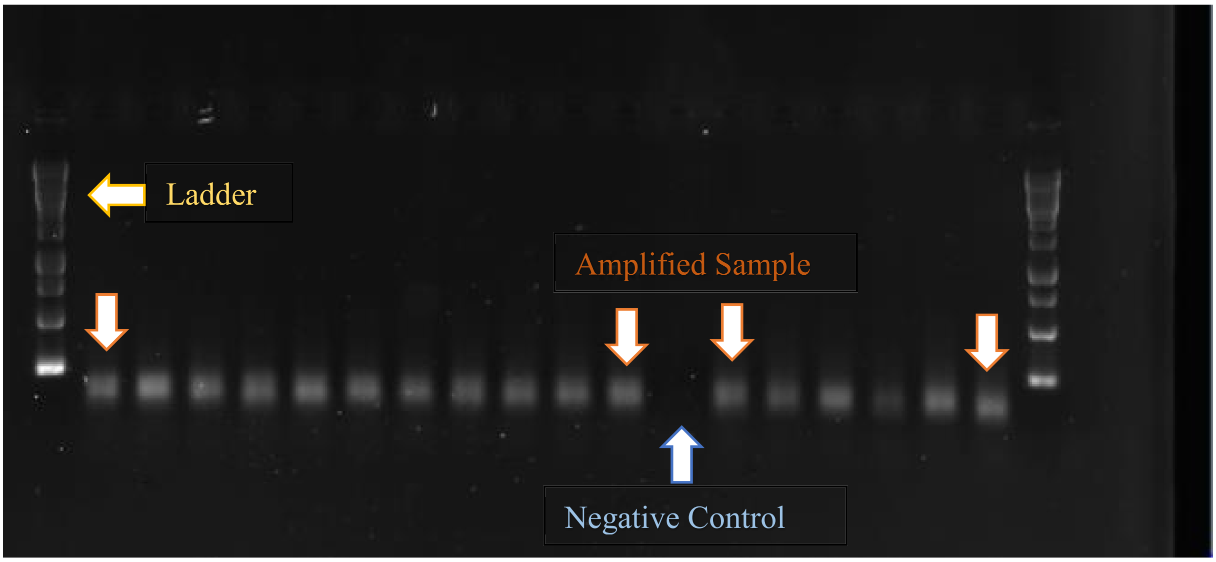


Figure 10. An example of an agarose gel after a PCR run. The negative control was filled just with distilled water, and hence it shouldn´t be amplified (blue arrow). On each side molecular-weight size marker, called ladder (100 bp Plus DNA 0,5 µg/µl,50µg) was added as well in order to see the length of the amplified PCR products (yellow arrow). Amplified samples (are marked with the red arrows). The electrophoresis run with the settings:

Next, -genotypes from 11 microsatellite loci from all 53 samples were analyzed with the software Genemapper. As shown in the example, a locus can be homozygous (Figure 11) or heterozygous (Figure 12) and alleles vary in length.

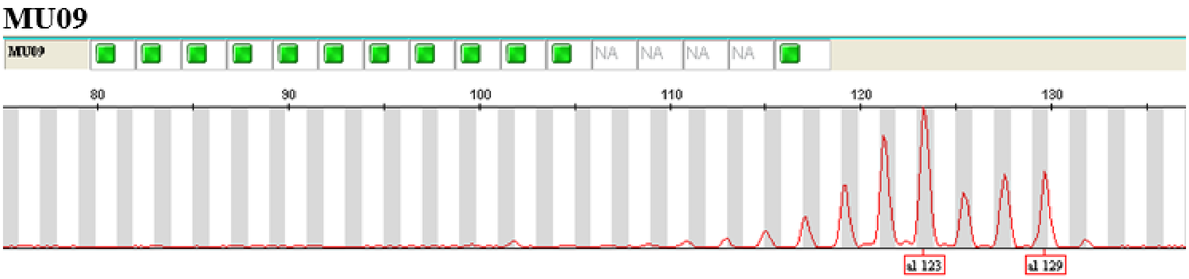


Figure 11. An example of a heterozygote genotype (with two alleles, 123 and 135) of MU09 locus using Genemapper program.

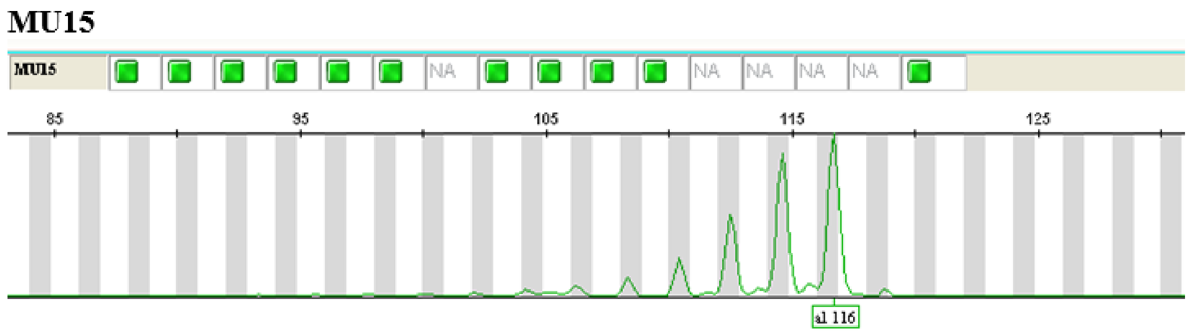


Figure 12. An example of a homozygote genotype (with two 116 alleles)

Based on the software GENAlex 11 microsatellites were used to estimate genetic variability (Nei, 1978). According to the results only 2 loci are enough to distinguish individuals from each other (Figure 13). In order to identify siblings reliably from each other using at a number of 4 loci is necessary. In conclusion, using 11 loci, is more than adequate to perform calculations of kinship relationships.

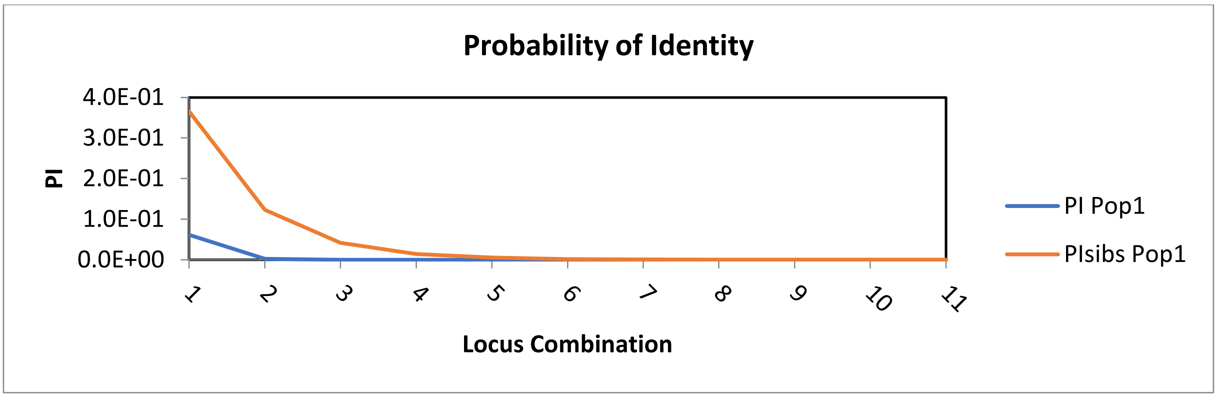


Figure 13. Probability of identity of 118 brown bears (*Ursus arctos*). Blue Line calculated the unbiased probability of identity (*PI*). Orange Line calculated the unbiased probability of siblings. Estimated by the software GENAlex in excel.

3.2 Genotyping error

It has been shown that the used loci for this study did not suggest just low allelic dropout or scoring errors in the microsatellite data (Kopatz et al., 2012). In other studies, from the same species with the same microsatellites, the genotyping error has been relatively low. For example in Sweden results show a genotyping error rate of ~ 0.8%. (Bellemain et al., 2006a; Waits et al., 2000) The most common sources of error in the studies were allelic dropout or human error (Pompanon et al., 2005).

3.3 Genetic variation

Genetic diversity of brown bear measured with allelic richness, (Ar) observed (Ho) and expected (He) heterozygosity and the inbreeding coefficient (Fis) were calculated from the 11 loci and is shown in the table 6.

Table 6: Estimated allelic richness (AR), observed heterozygosity (Ho), expected heterozygosity (He), inbreeding coefficient (F_{IS}) computed as in Weir & Cockerham (1984) and unbiased probability of identity (PI).

LOCUS	**CENTRAL (N=24)**				**EASTERN (N=29)**			
	Ar	Ho	He	Fis	Ar	Ho	He	Fis
MU05	6.000	0.792	0.839	-0.044	6.983	0.793	0.829	0.108
MU09	5.999	0.792	0.860	-0.107	9.923	0.793	0.824	0.161
MU15	10.869	0.750	0.803	0.207	11.032	0.724	0.892	0.135
G1D	5.999	0.875	0.828	-0.103	8.699	0.964	0.833	-0.124
G10B	5.999	0.783	0.823	0.052	10.261	0.828	0.773	-0.064
MU10	4.999	0.875	0.769	-0.178	6.754	0.929	0.793	-0.143
MU50	5.000	0.500	0.611	-0.172	10.035	0.625	0.522	0.099
MU51	9.000	0.750	0.801	0.338	11.187	0.571	0.866	0.197
MU59	15.000	0.957	0.899	-0.009	21.661	0.857	0.943	0.102
G1A	14.866	0.750	0.793	0.102	15.811	0.897	0.917	0.057
G10L	5.955	0.708	0.785	-0.080	7.661	0.759	0.719	0.067
MEAN	8.153	0.776	0.801	0.0312	10.909	0.795	0.810	0.019

In Eastern Finland, the mean expected heterozygosity was a little bit higher (He = 0.810) than in the Central Finland (He = 0.801). Furthermore, the values for the inbreeding coefficient are very low and have often negative value. Negative Fis values indicate that individuals in this population are less related than expected under a model of random mating (Frankham et al., 2010). The highest value was calculated in the central population at locus MU15 = 0.207. By using allelic richness and not the number of alleles, the values can be compared better since the values were corrected for the sample size. On average, the value in Central Finland (Ar = 8.153) was lower than in Eastern Finland (Ar = 10.909)

For the Finnish bear population structure, a Principal Coordinates Analysis (PCoA) (Figure 14) and a Geneplot (Figure 15) was carried out. The result of the PCoA shows that coordinate 1 explains 8.77% of the variation that seemed to divide large numbers of samples into eastern and central clusters. This divergence is very low and can be a result of isolation by distance.

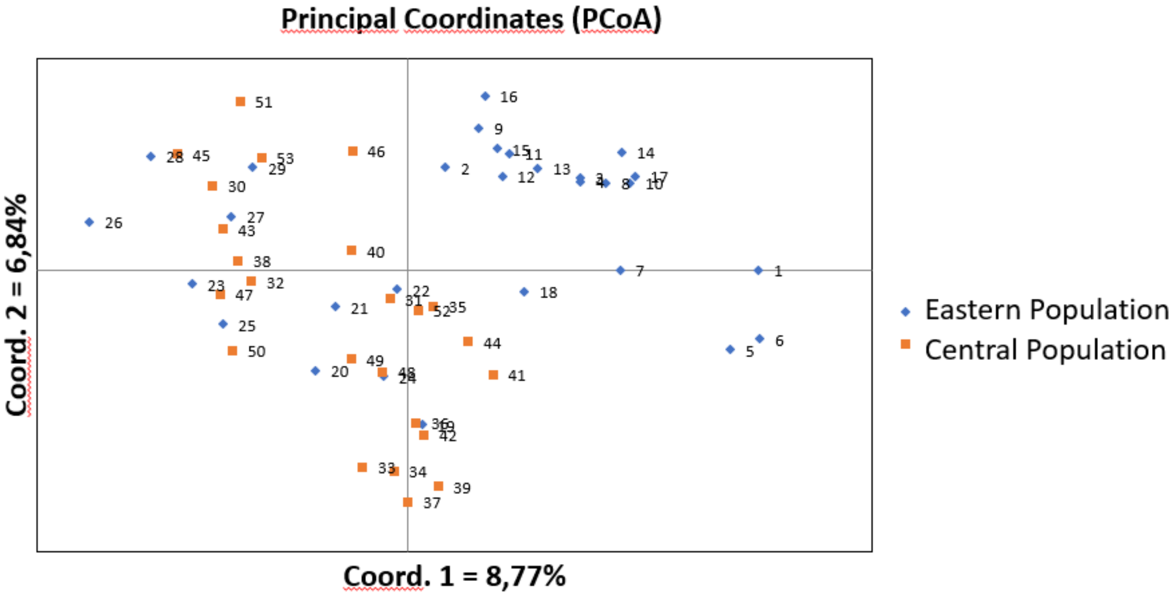


Figure 14: Estimated Principal Component Analysis of the Eastern Finland (Pop. 1) and the Central Finland (Pop. 2)

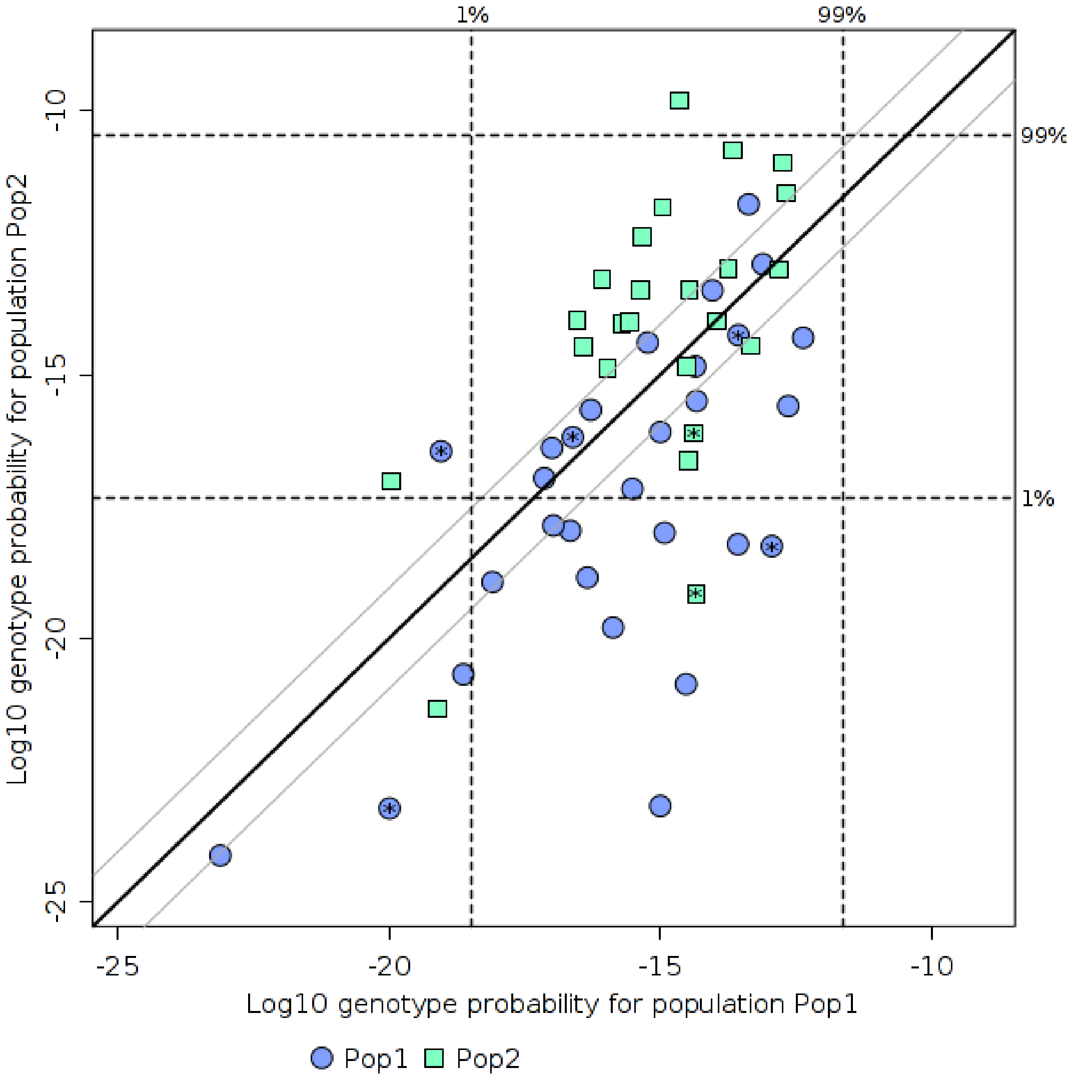


Figure 15: GenePlot based on microsatellite data. The graph shows bears sampled in Eastern (Pop. 1; blue circles) and Central (Pop. 2; green squares) Finland. Each point represents an individual bear. The X-axis shows the posterior log-probability of obtaining each individual's genotype from the Eastern Finland population; the Y-axis shows the posterior log-probability of obtaining each individual's genotype from the Central Finland population. The thick diagonal line shows equal probability with respect to Central and Eastern Finland population; the thin diagonal lines indicate that the probability is 9 times larger for one population than for the other. The vertical dashed lines show the 1% and 99% percentile log-genotype probability lines for the Eastern Finland population; the horizontal lines show the 1% and 99% percentile log-genotype probability lines for the Central Finland population. Bears marked with asterisks have missing data at one or more loci.

The X-axis of the Geneplot (Figure 15) shows the posterior log-probability (LGB) of obtaining each individual´s genotype from the Eastern Finland population: The Y-Axis shows the posterior log-probability of obtaining individual´s genotype from the Central Finland population.

Most of the bears seem to belong to the populations from which they were sampled. The horizontal and vertical dotted lines are the 1% and 99% quantiles of the posterior log probabilities. It is possible to observe in the figure 15 that all except four of the blue circle symbols (Eastern Finland) fit between the vertical 1% and 99% quantiles. Almost all except two LGB values for Central Finland brown bears (green square symbols) were also higher than the horizontal 1% log probability quantile.

The LGB-values could be used to access information on population structure. Most of the Central Finland brown bears had a high probability (Horizontal coordinate) to belong also to the Eastern bear population and only two of them had lower than 1% LGBs (Lower dashed vertical line). On the other hand, in general the Eastern Finland brown bears had on average lower probabilities (vertical coordinate) to belong to the Central Finland populations, and even 44.8% (N=13) of them had lower than 1% LGBs (Lower horizontal dashed line) to the Central Finland population. The Eastern Finland bears had more diverse LGP values with respect to both populations than the Central Finland bears reflecting observed higher genetic variation in the Eastern population. These patterns suggest that the Central Finland bear population is a genetic subset of the Eastern bear population.

The populations appeared not to be clearly separately clustered. The thick diagonal line is the equal posterior genotype probability for both populations. There were many individuals with almost equal probability to belong either of the populations. Four of the Central Finland bears had significantly higher probability to belong to the Eastern Finland population and two of the Eastern Finland population had significantly higher probability to belong to the Central Finland population. Three Central and one Eastern Finland population bears had a low probability to belong either of the two populations.

3.4 Kinship relationship

On average, brown bears are more closely related in Central Finland than brown bears in Eastern Finland (Figure 16) analyzed by software ML-Relate. The female bears were more closely related to each other in the center of Finland by a mean relatedness (max. likelihood 0.158) and clearly different than the brown bear population in the Eastern Finland in which the relatedness was low (max. likelihood 0.054). The difference between the two regions between male bears is not clear as the male mean relatedness is only 0.031 of the max likelihood higher in Central Finland.

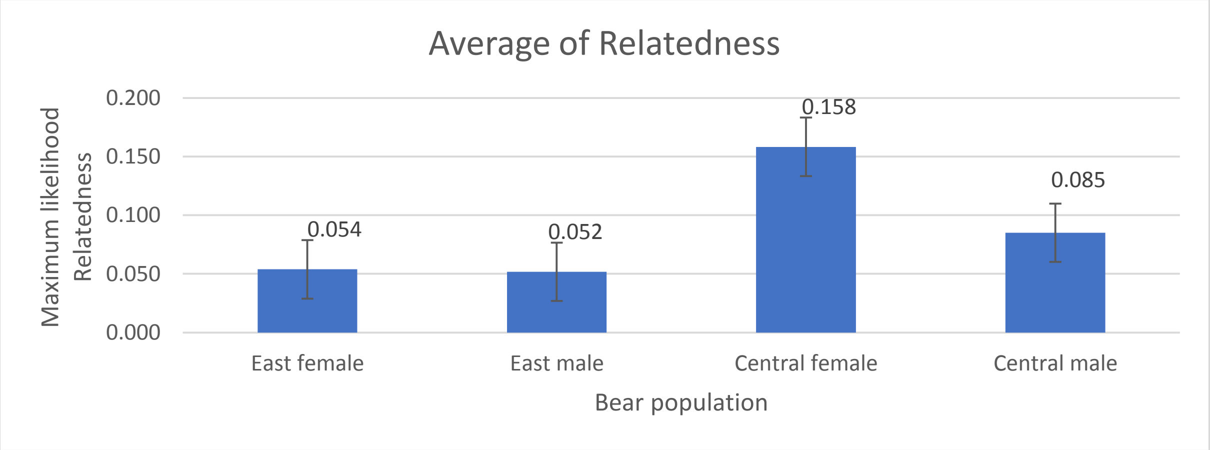


Figure 16: Estimated maximum likelihood of relatedness among the bear population. Divided in four groups: East-Female (N=13), East-Male (N=16), Central-Female (N=14), Central-Male (N=10). Calculated by the software ML-RELATE.

Based on the two-tailed t-test (t=3.4794; df =204.28; p = 0.0006) with a 95% confidence interval (0.022; 0.081) the mean relatedness of bears in Eastern Finland differ significantly from relatedness in bears in Central Finland. Also, when just female brown bears were used the relatedness was among the Eastern and Central Finland population clearly distinguishable (Figure 16) with t =3.8302; df = 140.7; p = 0.00019 of 95% confidence intervals (0.035; 0.11). On the contract, no clear difference in the relatedness between the male bears between Eastern and Central Finland could be identified (two-tailed test t = 0.64115; df = 60.64; p = 0.5238), which can be already seen from the error bars in the figure 16.

The software ML-Relate suggested several different relationship types between the individuals: half-siblings, full-siblings, mother-offspring. However, only one relationship could be confirmed from Luke`s field observation data. The female brown bear (Kaunotar; ID code: 6442) had two cubs in 2000. It is very likely that one of the cubs is the female (Domino: ID code: 5799).

3.5 Home ranges

A total amount of 82414 GPS locations from 39 brown bears in Eastern and Central Finland in the years between 2004 and 2014 from May until September was analyzed (Figure 17) in order to estimate kernel home ranges in the rank of 95%, 90% and 80%. A total amount of 94 kernel home ranges were estimated with HRT tool in ArcGIS Map (Figure 15). In average each home range kernel was estimated out of 887 GPS locations. Those home ranges can be split in 59 kernel home ranges in the central Finland and 35 kernel home ranges in east Finland. The home range were split also in 81 kernel home ranges of female brown bears and 13 kernel home ranges of male brown bears (Figure 18). The home range data was not normally distributed according to Shapiro Wilkox test (W = 0.64524, p-value = 9.715e-14).

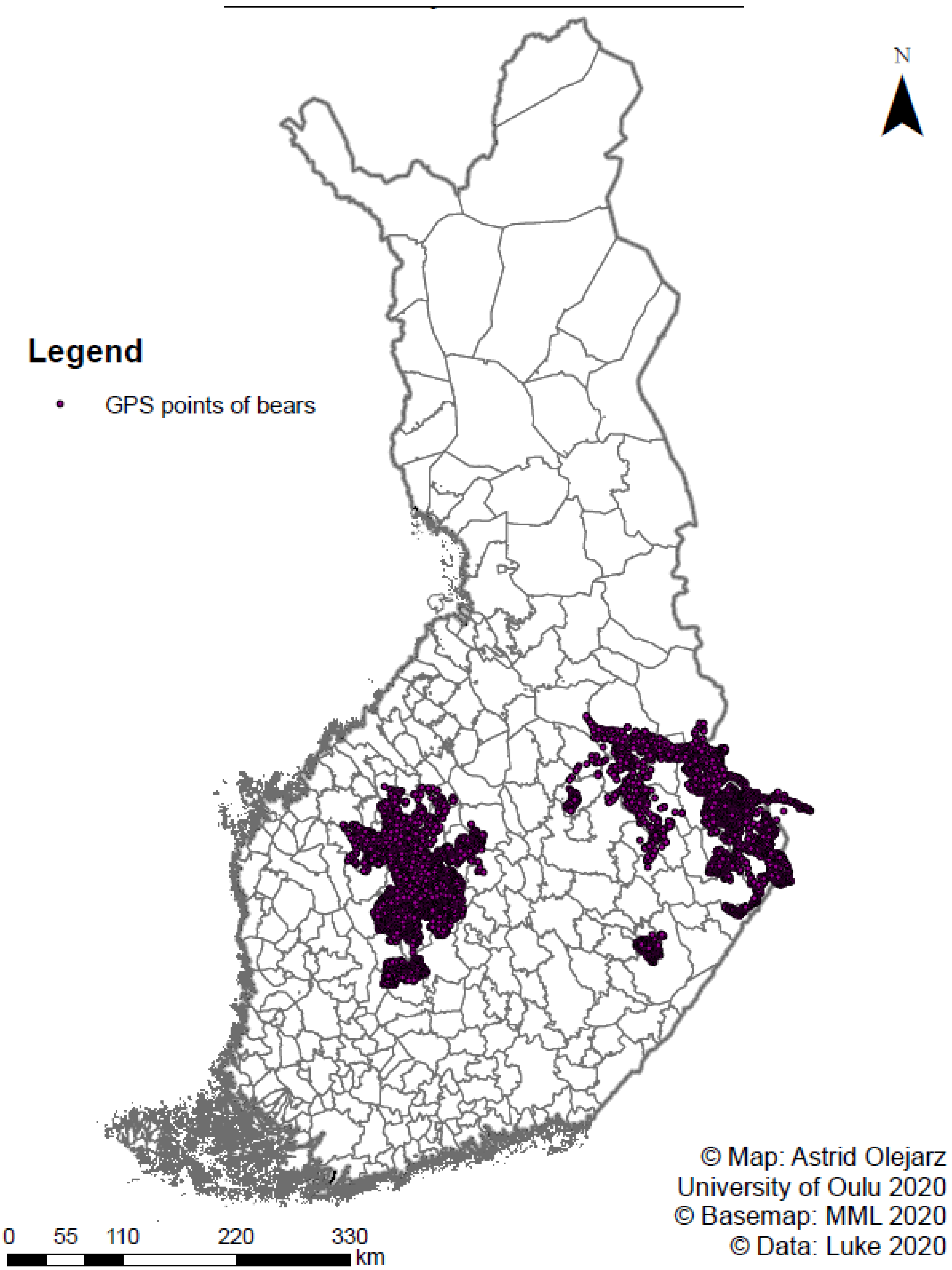


Figure 17: Map of the GPS locations of the monitored brown bears (*Ursus arctos*) in Finland. Created with ArcGIS Map.

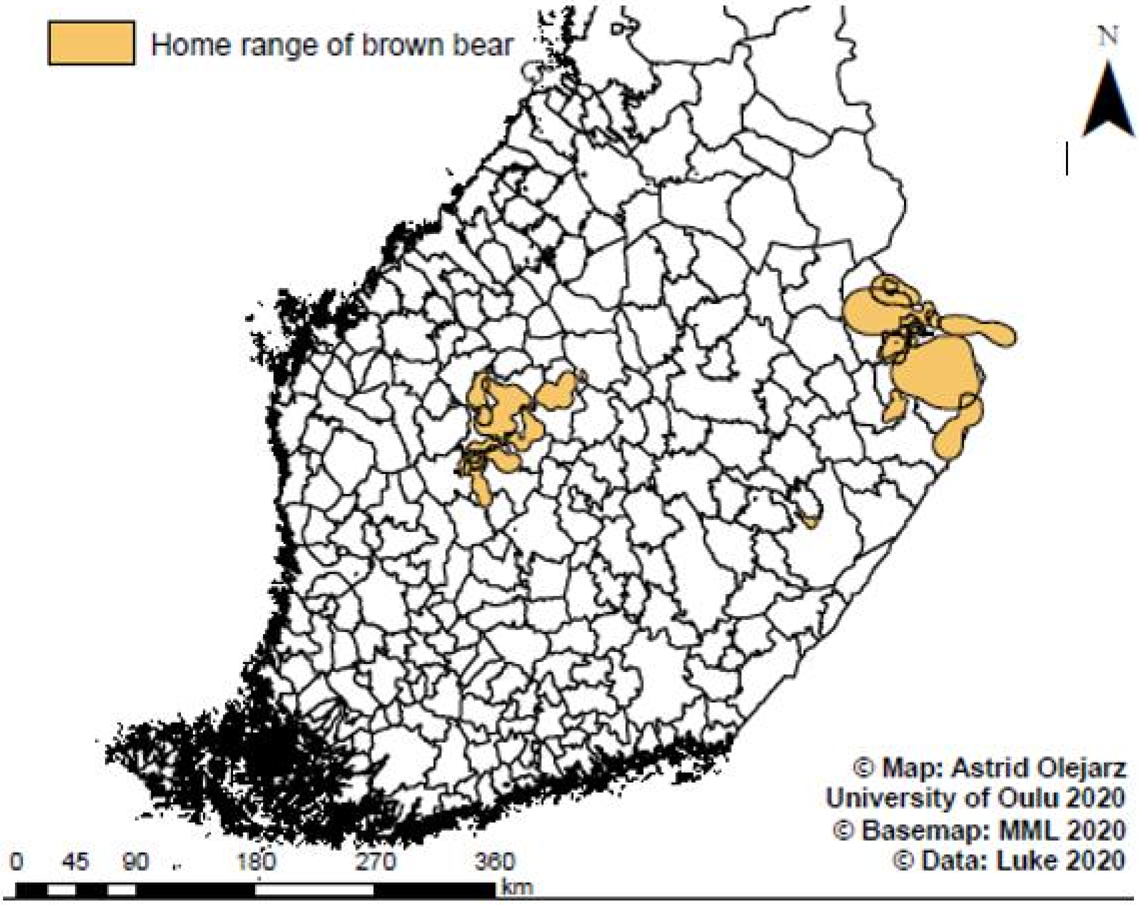


Figure 18: Map of Home range overlaps in the year 2011 between May and September with 90% of kernel estimation. Map created with ArcGIS Map

In average the size of the home ranges was significantly smaller in female compared to male brown bears, analyzed by the Mann-Whitney-U-Test (W = 969; p=1.292e-06) (Figure 19). A significant difference between the home ranges in eastern and Central Finland could be not detected by the two tailed t-test. Kernel home range of the female brown bears in Finland was smaller than the kernel home range of the female brown bears in central Finland (W = 125; p=4.262e-09). Comparing the kernel home ranges of the females with cub and females without cubs, the two tailed t-test (W = 603; p=0.4422) gave few supports to the idea, that the home range of females with cubs is smaller than from female without cubs (Figure 20).

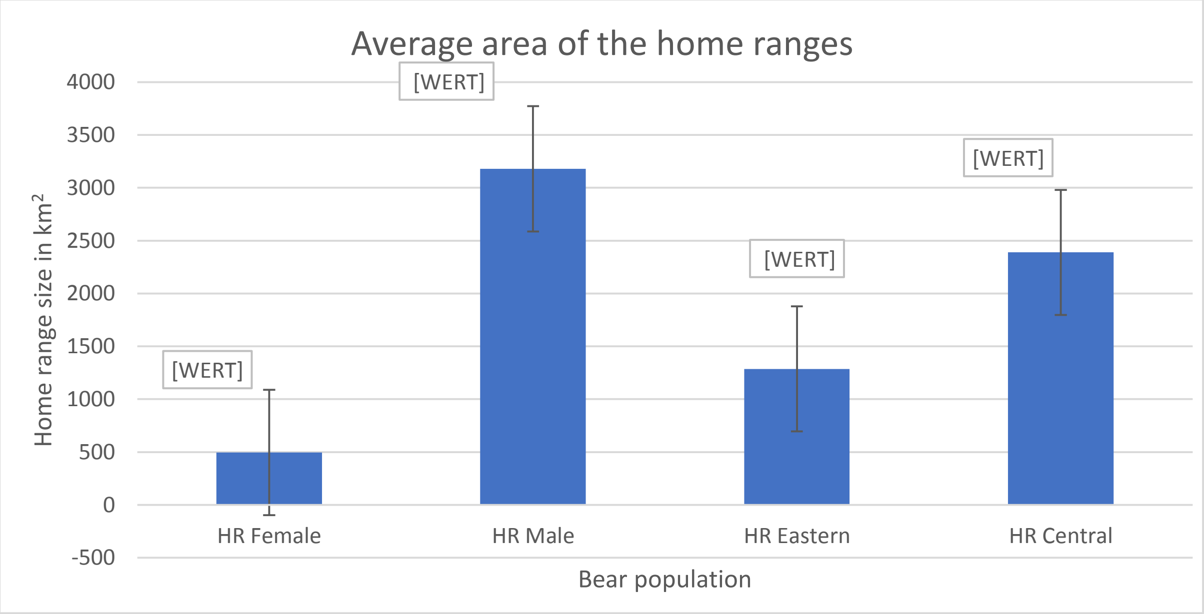


Figure 19: Estimated home ranges among the bear population. Divided in four groups: Home range Female (HR Female) with N=81, Home range Male with N=13, Home range Eastern Finland (N=35), Home range Central Finland (N=59). Calculated by the software ArcGIS.

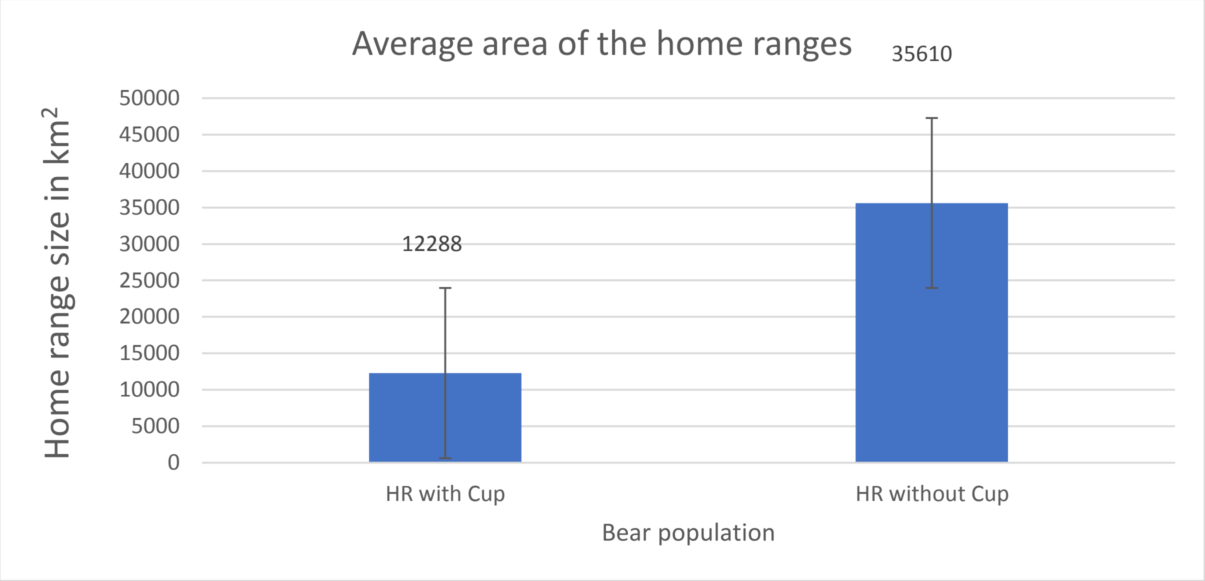


Figure 20: Estimated home ranges among the female bear population. Divided in two groups: Home range with Cup with (N=26), Home range without Cup (N=55). Calculated by the software ArcGIS.

3.6 Overlap of home ranges

Analyzing all calculated home ranges of bears, it came out that 19 home ranges out of 94 had no overlaps with other collared brown bears. In total an amount of 110 home range overlaps between a pair of two brown bear individuals has been detected in ArcGIS using 90% of kernel estimation (Figure 18). Home ranges overlapped 86 times in Central Finland and 24 times in Eastern Finland. The highest number of overlaps of two home ranges existed between two females (N=78). Home ranges of a female and a male bear overlapped 26 times. The fewest number of overlaps of two home ranges was found between males (N=6). An example of home range overlaps between three female brown bears in central Finland is shown in Figure 21.

GPS data of radio collared brown bears in Finland has been collected between the years 2004 until 2014, but no overlaps could have been detected with ArcGIS analysis for the year 2004 and 2007. Most home range overlaps has been detected in the years 2010, 2011 and 2012 with an average of 27 home range overlaps per year among 29 brown bear individuals.

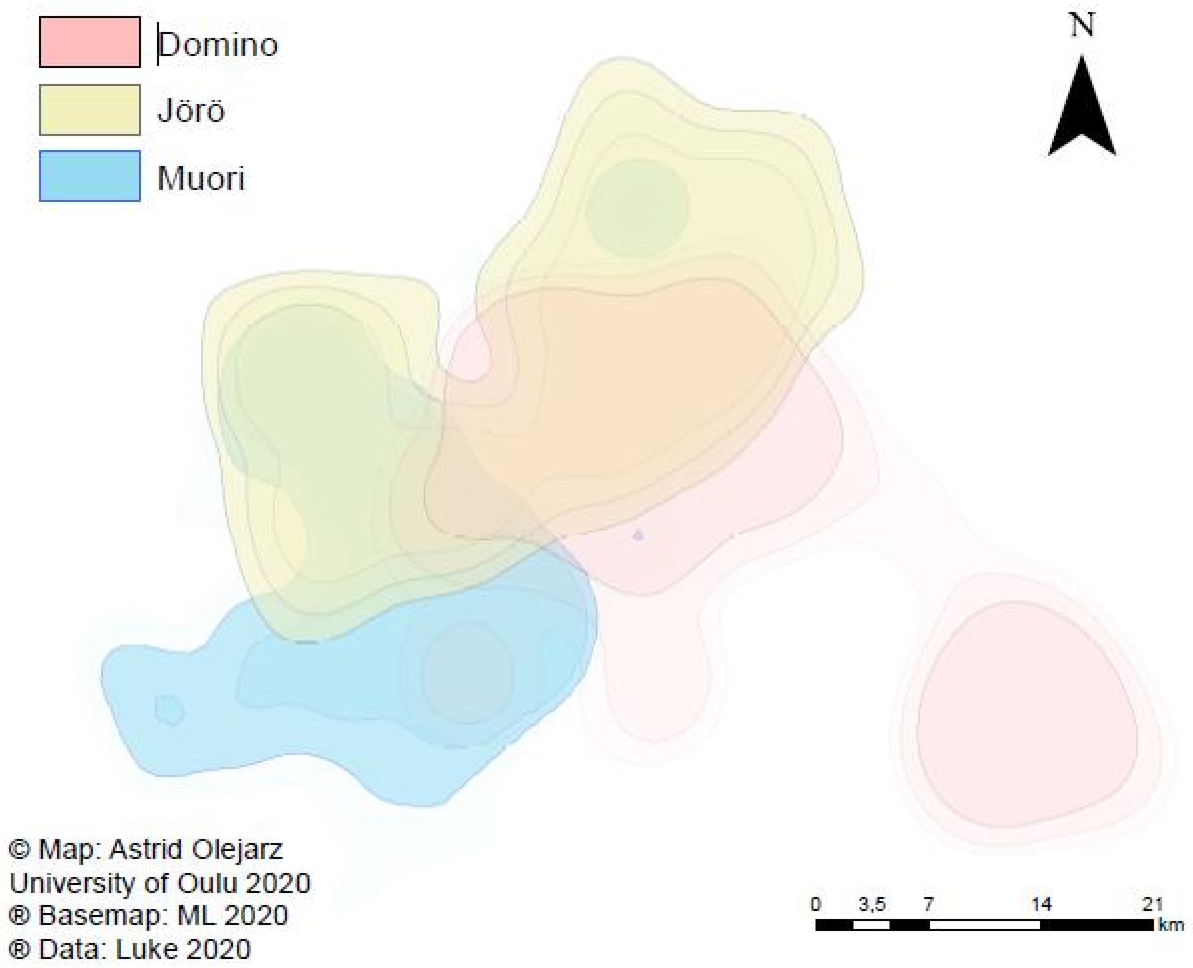


Figure 21: Map of three female brown bears in central Finland in the year 2011 between May and September. Kernel Home Range has been calculated by 95%, 90% and 80% of sample points. Map created with ArcGIS Map.

3.7 Home range overlap and the relatedness of the bears

The overall Spearman correlation between the overlap of home ranges with the degree of relatedness (Figure 22) using all overlaps (N=110; 39 bear individuals) between 2004 and 2014 was $\rho = 0.23$; p 0.0.152.

In a more detailed analysis, the overlaps of the home ranges were analyzed separately for each year from 2004 to 2014. In a few years, such as in 2004 and 2007, no overlaps of home ranges could be measured because there were not enough collared bears to produce sufficient amount of data. In some study years, (2005, 2006, 2008, 2009, 2013 and 2014) there was only a small number of overlaps, and thus not significant meaningful correlations between home range overlap and degree of relatedness could be estimated. Only in the years 2010, 2011 and 2012 there were an average of 27 overlaps per year, that is enough estimate correlation for a given year. The strongest positive correlation $\rho = 0.45$; $p=0.0173$ was measured in 2010 (Figure 22).

When the total home range overlaps are divided into the regions of Eastern Finland ($N = 24$) and Central Finland ($N = 86$), both regions have a positive correlation between home range overlap and degree of relatedness. Neither the region in the east ($\rho = 0.09$; $p = 0.6646$) or the region in the center ($\rho = 0.17$; $p = 0.1271$) had a p-value below 0.05, which is considered a significant value for the correlation (Figure 22).

Finally, the correlation between the same or different sexes of bears and the number of home range overlap was examined. The home range overlaps were divided into female-female overlaps ($N = 78$), female-male overlaps ($N = 6$) and male-male overlaps ($N = 26$). Due to the low number of GPS coordinates and the resulting small number of home ranges, the analyzes with the male bears did not provide any statistically relevant data. However, in the analysis among the female bears, there was a positive correlation ($\rho =0.24$; $p =0.0379$) between the overlap of the home ranges with the degree of relatedness (Figure 22).

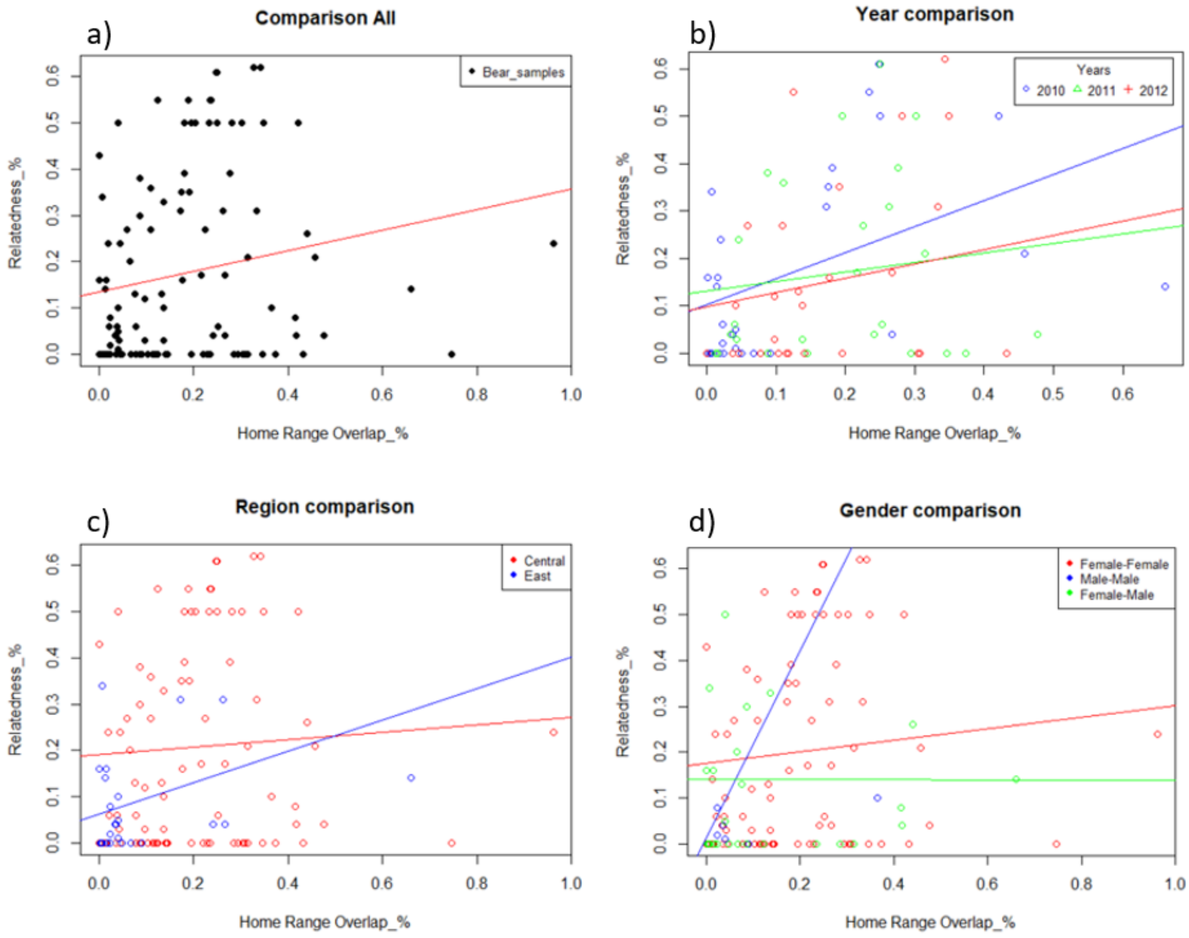


Figure 22: Relationship between the home range overlap and relatedness; a) Number of home range overlaps (N = 110), b) Comparison between the most significant years 2010 (N=28), 2011 (N=25) and 2012 (N=28), c) Comparison between the two regions Eastern Finland (N=24) and Central Finland (N=86), d) Comparison between the genders, with just the most significant gender comparison female-female (N=78).

4 Discussion

4.1 Assessment of invasive and non-invasive methods

The aim of this master thesis was to uncover social structures among the bears. In order to tackle such a complex topic, basic genetic parameter of each individual brown bear and two specific characteristics from the bear structure were analyzed: on the one hand the degree of kinship among the bears and on the other hand the overlap of the individual home ranges.

Basic parameters such as age and gender are easy to determine if the pedigree of a population is known and they are under constant monitoring. However, this can be challenging in the case of large carnivore, as they usually live secretive, solitary occur in low densities and have large home ranges (Kindberg et al., 2009). Often the age and the sex of some animal species cannot simply be morphologically determined from distance. A very good approach to determine the basic parameters is the invasive method. The animal is tracked by helicopter and anesthetized. This allows the scientists to safely approach the animal and take measurements directly on the animal. Gender can easily be determined based on the genital organs. The age can be determined on the premolar tooth. After the examination, the animal is de-anesthetized by an experienced veterinarian. As simple as the method sounds, the method of preparation is very costly and bureaucratically intensive. This is one of the many reasons why more and more parameters are taken using non-invasive methods in bears (Berezowska-Cnota et al., 2017) but also in wolves (Aspi et al., 2009) and wolverines (Cegelski et al., 2006). By only collecting animal samples in a way that avoids direct contact with the animal, their normal behavior of the studied animal is not going to be disturbed. (Norman 2015)

For population monitoring and the estimation of important population genetic parameters it is no longer necessary to have high-quality samples, but samples of feces or hair are also sufficient (Bellemain et al., 2005). Laboratory analyzes have become more precise and less expensive, and new software has been developed that specializes in the evaluation of the quality of genetic data. Many population structure analyses of certain wild animals are nowadays only based on non-invasive methods (Cegelski et al., 2006). In this work, all samples come from high-quality samples taken directly from the bear, using an invasive capture method, and that is why all samples could have been identified by their genetic relationships. However, it might have been enough for the kinship analysis to collect just hair and fecal samples of the respective bears in the areas.

The spatial distribution of large carnivores is often very difficult to analyze. This is caused by the fact that large carnivores such as brown bears often inhabit large areas. Following their tracks at a close range is very dangerous. (Norman and Spong, 2015). With the help of GPS collars, it is not only possible to cover and analyze a large home ranges of an brown bear, but also to investigate migration behavior (Norman and Spong, 2015). GPS collars often send easily evaluable and exact data about the animal's habitat over several months, if not even years. As soon as the battery is empty, the collar detaches from the animal and it can usually be safely collected and reused by the scientist. If the GPS collar works correctly, it sends a lot of easily evaluable data. On average, 887 GPS positions were assigned to each individual home range of a bear in this master thesis. Unfortunately, we did not get this much data from each bear. Out of the 53 bears that were analyzed in this thesis, we got GPS coordinates from 39 bears. There have also been attempts in other bear projects to try to determine the home range of bears using non-invasive methods. Bear feces and hair samples were collected. Each sample collected was noted with the corresponding GPS position. However, the method has two major disadvantages to a GPS collar. On the one hand, each sample has to be clearly assigned to an individual in the laboratory. On the other hand, the amount of data from a collected material is significantly less than when a GPS collar sends a location position every hour on average. Studies have shown that the less GPS material is available, the more likely it is that an animal's home range will be underestimated (Bellemain et al., 2005; Solberg et al., 2006).

4.2 Genetic variation

With the help of observed and expected heterozygosity analyzes, it is possible to determine the genetic diversity in the bear population. It provides information about certain historical events such as population bottleneck or metapopulation dynamics. The Finnish bears showed a relatively high mean in the observed as well as in the expected heterozygosity in comparison to other brown bear population in the world (Table 7). This shows that there is a relatively high level of genetic variability in the population and that the population have not gone through recent bottleneck. The genetic diversity values are similar than in other publications about the Finnish brown bear (Kopatz et al., 2012).

Table 7: Comparison of the genetic diversity measured among studied subpopulations (**bold**) and other published brown bear populations based on microsatellite data including sample size (N), number of locus used (L), mean number of alleles per locus (A), observed heterozygosity (H_o) and expected heterozygosity (H_e)

Population	**N**	**L**	H_o	H_e	**Reference**
Romania	109	13	0.72	0.81	Zachos et al., 2008
Croatia (Dinaric Mountain)	156	12	0.74	0.75	Kocijan et al., 2011
North America (Yellowstone)	57	8	0.55	0.55	Paetkau et al., 1998
Pakistan	28	15	0.56	0.55	Bellemain et al., 2007
Italy (Apennines)	30	12	0.40	0.44	Lorenzini et al., 2004
Spain (Western Cantabrian)	39	18	0.44	0.45	Pérez et al., 2009
Scandinavia M	88	19	0.65	0.66	Waits et al., 2000
Scandinavia NN	29	19	0.66	0.66	Waits et al., 2000
Scandinavia S	155	19	0.76	0.66	Waits et al., 2000
Northern Slovakia	71	13	0.69	0.71	Straka et al., 2012
Central Slovakia	96	13	0.69	0.70	Straka et al., 2012
Eastern Slovakia	16	13	0.66	0.65	Straka et al., 2012
Eastern Finland	29	11	0.79	0.81	**This study**
Central Finland	24	11	0.77	0.79	**This study**

In addition to the estimates of observed and expected heterozygosity, the inbreeding coefficient (F_{IS}) was also determined. It can be used to determine the reduction in heterozygosity of an individual due to non-random mating within its subpopulation within one generation and to suggest out of this, whether inbreeding has taken place among the population. Especially small populations with a small number of individuals often have a high inbreeding coefficient because there are not enough different reproductive partners available. The consequences are that genetic diversity is lost and phenotypic features of recessive alleles that lead to genetic diseases can expressed more easily. This phenomenon can be observed in part in the Swedish wolf population due to its small number of individuals (Aspi et al., 2009; Räikkönen et al., 2013). This phenomenon can also be observed in some other large carnivore species such as the amur tiger (Wang et al., 2016). However, the brown bear population in Finland does not appear to suffer from these problems, since the F_{IS} value is low and does not indicate any inbreeding (Hagen, 2015). The publication from Kopatz et al. (2012) even claims that the low F_{IS} value for brown bears in Finland is a sign that there is an intensive migration between Finnish and Karelia bear populations (Hagen et al., 2015). There has been constant increase in the population size since the late 1960 (Kojola and Heikkinen, 2006). It seems that old fences from the Soviet era does not prevent the migration between the two countries as it supposed to be for wolves (Aspi et al., 2009).

Allelic richness is another measure of a population's genetic diversity. It is used less often than heterozygosity as a measure of genetic diversity, partly because it is more difficult to calculate mathematically. Based on the results, it can be concluded that in the long term there is potential of the brown bear population to adapt and persist in the genetic point of view. Unlike in the other two genetic diversity measurements. There is difference in allelic richness between the central and eastern population. In the east the allelic richness seems to be higher than in the central part of Finland, which is an indication that the Central Finland bear population was a genetic subset of the Eastern Finland bear population. In the time of recolonization of Central Finland some genetic diversity could have been lost. Furthermore Eastern Finland has a higher population density, which lead often also to a higher allelic richness (Hagen, 2015). In Saarma et al. 2007 it was estimated that there are 40 000 brown bears in northeastern Europe and that in Finland most of brown bears are living along the Russian border (Saarma and Kojola, 2007). Gene flow exist from the Karelian population in Russia (Kopatz et al., 2012).

Also, interesting to observe is, that if all genetic information from both regions are compared with each other in a principal component analysis, a low level of differentiation can be observed between east and central Finnish brown bear population of by the first principal component (8,77%). This may have arisen from the fact that the bears in central Finland are not as exposed to extreme migration from Russia as the bears in the east (Kojola and Heikkinen, 2006). In general, subadult male bears show natal dispersal (Kojola and Heikkinen, 2006). Female bears seem to be more philopatric and create an own new home rage close to the natal area. Only when the population density is high female brown bears start to disperse to new home ranges (Ordiz et al., 2008).

Furthermore, the patterns from the Geneplot analysis shows that the brown bears from Eastern Finland had a more diverse LGB values with respect to both populations than the brown bears from Central Finland. Most of the Central Finland bears had high LGP with respect to the Eastern Finland population (horizontal coordinate), and thus could plausibly have originated in Eastern Finland population, whereas very few of the Eastern Finland bears had high LGP with respect to the Central Finland population (vertical coordinate). These patterns suggest that the Central Finland population is a genetic subset of the Eastern Finland population. The populations were not highly diverged, as four of the of the Central Finland bears had significantly higher probability to belong to the Eastern Finland population and two of the Eastern Finland bears had significantly higher probability to belong to Central Finland population. This observation support recent migration between the two populations. Migration in brown bears is density dependent (Ordiz et al., 2008). The high dense population in Eastern Finland is more migrating to the low dense population in Central Finland than vice versa. Three Central and one Eastern Finland population bears had a low probability to belong either of the two populations suggesting that they are originally coming outside of the study areas.

4.3 Kinship relatedness

The results show that the degree of relatedness among bears in the Central Finland is higher than among bears in eastern Finland. This is most likely because the bear density in the Eastern is significantly higher than in the Central Finland (Hagen, 2015). A higher population density normally causes lower relatedness between the individuals (Kawata, 1990). Another factor is that the bear population in the east is more exposed to bear migration from Russia (Kojola and Heikkinen, 2006).

Interestingly, if we analyze sexes separately, it can be observed that the difference in the kinship level was considerable higher in the female brown bears in the Central Finland by a mean relatedness (max. Likelihood 0.158) compared to Eastern Finland by a mean relatedness (max. Likelihood 0.054). Male bears were less related less with one another male bear. This can be explained by two behavioral reasons: First, male bears tend to have the characteristic to disperse from their natal place in order to find new home ranges with new potential mating partners (Støen et al., 2006). Natal dispersal is defined as the movement of progeny from the birthplace (the natal area) to the area where it reproduces (the breeding area) (Greenwood, 1980). This characteristic trait is important among bears because it naturally prevents inbreeding. It was not only observed in brown bears but also in other large carnivores, such as cougars (Sweanor et al., 2000).

Second, young female brown bears tend to stay close to their natal place. The mother brown bear seems to tolerate more their own offspring. A possible explanation could be that this tolerance can continue to ensure that the offspring survive and increase their own fitness. However, a high female bear density like in the Eastern Finland (Hagen, 2015) can suppress this behavior, because good quality home ranges are hard to acquire due to the high competition among bears If two dominant unrelated female brown bears have home ranges close next to each other, there will be no space to establish a new home range for the offspring close to the mother. Thus, female offspring adult brown bears would be forced to find a home range further away from the mother area. Dispersal can have an effect on conservation issues such as inbreeding and population genetic structure (Greenwood, 1980). A decrease in kinship with increasing population density can be observed not only in bears, but also in voles (Kawata, 1990).

4.4 Home range

While the bear population was greatly reduced by the beginning of the 20th century, the presence of brown bears was focused just to the eastern part of Finland (Hagen et al, 2015). Only through strong protection of the bear population by the Finnish government the population was able to recover in other areas of Finland (Hagen et al, 2015). The regeneration of the brown bear population is a long-time consuming process. Brown bear species have a long generation time and a slowly growth rate (Kopatz et al., 2012). When an adult bear has acquitted a home range it will stay there for most of his live, if no strong changes such as human disturbances or lack of food availability will occur (Danilov, 1994). However, the distribution of the bear population in Finland is still not even. The density of brown bears in Central Finland is much lower than in Eastern Finland (Kojola et al., 2007). The northern parts of Finland consist with even lower density of the brown bear population as in Central Finland as no protection existed in northern areas for bears and poaching of bears is still very common, because of reindeer herding (Kojola et al., 2007). Over the years, a stable bear population has been established itself again in two areas of Finland: one in the Central Finland and the other in the Eastern Finland. GPS tracking of radio collared brown bears shows that their home ranges differ significantly between the two areas. Bears in Eastern Finland appear to have smaller home ranges on average than bears in Central Finland.

In the east, the area close to Russian border has no human activity and there is diverse fauna (Saarma and Kojola, 2007). This rich habitat for bears has the advantage that bears just need to establish a small home range (Mcloughlin et al., 2000). A good habitat for a bear population consist either of spruce forest or mixed forest (Danilov, 1994). Those areas are able to maintain a higher bear density without exhausting the carrying capacity of the environment. Home ranges are not only selected based on the good food supply, but also based on minimum human disturbance. Bears try to avoid human settlements, not just because of the fact that forestry and agriculture reduce the food supply (Schregel et al., 2012), but also because bears naturally try to avoid human contact (Nellemann et al., 2007). Central Finland have a relative higher human density than Eastern Finland (Rapo, 2012). In the same way, the human disturbance to nature is significantly higher in central Finland, for example with forestry and agriculture. Bears tend to well adapted to a various of habitats, nevertheless agricultural fields with pastures seems not belong to the preferable habitats (Danilov, 1994). This can be a possible explanation that bears have a larger home range in Central Finland so that they have enough resting places as well as enough food.

The difference in the home ranges is not only between the two regions in Finland, but also in comparison to other regions of the world (Table 8). There is large variation in the home ranges between the countries due to some differences. Measurements of home range size vary between the studies. Mostly the calculation used kernel home ranges in ArcGIS to determine the home range. The calculated kernel ranges were varying between 90% and 95% (Penteriani et al., 2017a; Støen et al., 2005) and this study. Other publications used different measurements such like minimum convex polygon (MCP) to determine the home range (Blanchard and Knight, 1991; Kaczensky et al., 2003). Also, human population density and their presence in the nature differ greatly among the countries. Home range sizes could be strongly affected by the presence of humans and their previous experience of the individual bear with them (Pop et al., 2012). As already shown in this study, brown bear density and food availability play an important role in the home range size. Habitats with good food supply decrease the need of large home ranges (Mcloughlin et al., 2000). Food resources are not equal distributed, in space and time so that in some areas brown bears need to have bigger home ranges than in others (Begon et al., 2006).

Furthermore, this study shows that the male bears have a larger home range than the female bears (Figure 19). The need for male bears to have a larger home range is because of several factors: 1) Male bears are larger than female bears. As a result, they have a significantly higher nutrition consumption and are so on more dependent on high-quality living areas. This can be achieved by the male bears by simply increasing the bear's home range (Bellemain et al., 2006a). 2) Another important factor is that the male bear increases their own fitness by reproducing with as many females as possible. Male bears are not involved in the rearing of offspring. Thus, their successful reproductive strategy is based on mating with as many females as possible during the mating season. It can happen that an offspring from the last year is going to be killed by a male brown bear, in form of a “sexually selected infanticide (SSI), so that the new dominant male can mate earlier with the female brown bear (Bellemain et al., 2006a). Female brown bears that has lost its cub gets the estrus cycle faster and is willing to mate again. An important factor for SSI strategy of male brown bears is that male brown bears are just killing unrelated offspring, perhaps by recognizing the females they mated with the year before (Bellemain et al., 2006a). Infanticide seems not just a common strategy for brown bears, but also in other large carnivores such as social species for example lions (Packer and Pusey, 1983) and solitary species for example leopards (Balme and Hunter, 2013). Females, on the other hand, can live with smaller and less nutritious habitats due to their smaller size. The cost of rearing offspring is just under the responsibility of the mother. The success of her fitness is not due to the number of reproductive options but the successful rearing of her offspring. In general, an offspring stays with the mother for 1 until 3 years (McLellan et al., 1994). Only after that the female bear is able to have new cubs (Dahle and Swenson, 2003c).

Table 8: Comparison of the home ranges in km^2 measured among studied subpopulations (**bold**) and other published brown bear populations based on GPS coordinates including number of home ranges (N), divided in female home range (F) and Male home range (M).

Population	N	F	M	Reference
Scandinavia	37	437	-	Støen et al., 2005
North America	35	2577	-	Mcloughlin et al., 2000
North America (Yellowstone)	41	884(21)	3757(20)	Blanchard and Knight, 1991
Scandinavia (South)	61	217(34)	10755(27)	Dahle and Swenson, 2003b
Scandinvia (North)	27	280(18)	833(9)	Dahle and Swenson, 2003b
Spain	1	28.16	-	Penteriani et al., 2017
Croatia	9	58(5)	128(4)	Huber, 1993
Japan (Hokkaido)	3	43.04	-	Sato et al., 2008
North America (Alaska)	20	356	-	Collins et al., 2005
Slovenia	6	53(5)	237(1)	Kaczensky et al., 2003
Eastern Finland	35	127(25)	2445(10)	**This study**
Central Finland	59	862(56)	3914(3)	**This study**

These different reproductive successes cause a conflict between the two sexes in the bears (Dahle and Swenson, 2003c). The male brown bear tries to increase his fitness by having many mating partners each year and thereby increasing his home range. Female brown bears try successfully to raise the offspring every 2-3 years without getting into the range of other unrelated male bears. For this reason, female with cubs minimize the size of their home ranges, move shorter distances, are less active and use different habitats (Ordiz et al., 2008).

This slight tendency of an additional reduction in home range during the time the mother is rearing the cubs could be studied using GPS collared female bears. In some publications it has even been reported that during estrus female bears that do not have young offspring also show a tendency to roam to mate and thus to increase their home range in order to find the best mating partner for the next offspring (Dahle and Swenson, 2003c). This roam to mate behavior and increasing home range should be observable between the mating season during early May till mid of July (Bellemain et al., 2006a; Mcloughlin et al., 2000). It has even been observed that some females mate with several different males, in order to decrease the risk of infanticide of the next year cubs. Cub mortality seem to be very present in an area of a high brown bear density (Bellemain et al., 2006a). However, no statistical significance for the increase of female home ranges during the mating season could be demonstrated with this data.

4.5 Overlap of home ranges

When analyzing the bears' home range kernels with the software ArcGIS, it turned out that almost every bear had an overlap of its home range with other bears. Out of the 94 home ranges, only 19 home ranges had no overlap with other home ranges. However, we studied only a fraction of brown bears living in Finland. The probability that these home ranges also overlap with other home ranges is high. In Finland there are around 2020-2130 brown bears (Heikkinen et al., 2018) and this study involves only home ranges of 39 brown bears.

Generally, it can be said that brown bears tolerate overlaps of home ranges. This must be because there are certain benefits from it. Overlaps are an indication that the overlapping home ranges have good food sources (Mcloughlin et al., 2000) High food availability leads often in brown bears to an increase in the density (Jerina et al., 2013). In North America grizzly bears overlap in their home range during the season of high salmon abundance and there is no aggressive behavior between bear individuals (Mcloughlin et al., 2000). The high level of acceptance comes from the fact that the food supply has to be greater than the hunger of the bears. Such a tolerance can also be observed in Europe in home range overlap, for example at feeding stations of wild animal (Kavčič et al., 2013). Food availability is the primary reason that home ranges overlap. This phenomenon can be observed not only in bears, but also in other mammals such as coyotes (Atwood and Weeks, 2003) or cougars (Elbroch et al., 2016).

Furthermore, the analyses with ArcGIS shows that most of the overlaps took place between female bears (female-female) with a total amount of 78 calculated overlaps. However, this statement is not very representative of the actual ratio of overlaps, since the proportions between female and male bears were not equally distributed due to incorrect GPS measurements in male bears with GPS collars. It is known that due to their reproductive behavior, that male bears tend roam to mate, male bears have more overlaps of home ranges with females than between female-female and male-male (Dahle and Swenson, 2003a). In order to confirm these observations in this work, further evaluations of home ranges of male bears with GPS collars would have been necessary.

4.6 Social structures

The Spearman correlation between the degree of relationship and the overlap of the home ranges showed a positive correlation with each other ($\rho = 0.23$) and a p-value of $p = 0.0152$. Brown bears that are more closely related to each other are more likely to accept each other in their own home ranges than unrelated bears. This means that brown bears change their social behavior to less aggressive depending on the degree of kinship to other brown bears and are accepting home range overlaps not just because of abundance of food sources. However, this social behavior must bring advantages among related members of the same species and create a social network structure with an increased fitness for both individuals (Kawata, 1990; Krause et al., 2009).

Positive relationship between home range overlap and relatedness seems to be largely due to female-female interactions ($\rho = 0.24$) with a p-value of $p = 0.0379$. The closer the two females are related to each other, the more you can see an overlap between the two home ranges. Females tend not to move as far from their natal area to create their own home range. This decision has the advantage that young female brown bears are improving its own quality of life by sharing the mother's high-quality home range (Ramos-Fernández et al., 2006). The mother also benefits from living in close contact with its daughter. On the one hand, it ensures that its own offspring survive in the long term. On the other hand, the mother brown bear is safe from other dominant females who could dispute the area because it is surrounded closely related females. Some publications even claim that the dominant female, mostly the mother, can suppress the other females in their environment (McLellan and Hovey, 2001). Only the dominant one can have offspring in a certain year as a form of strategy to increase the chance of the survival of their own offspring. This suppression of the dominant female has been reported mostly in large carnivores that lives in packs like wolf packs (Peterson et al., 2002). Dominant females are usually older brown bears, so that it seems that age structure has also some influence for this social organization. Social organizations based on age has been observed in elephants (Wittemyer et al., 2005). Male bears will pay less attention to her cub, because the male bear will roam to mate with the other females and so those cubs will be protected from infanticide. This coordination between the birth years of the young animals could generally increase the reproductive success of the bears. A social interaction in the rearing of the offspring is actually only known in mammals living in social groups, such as spotted hyenas (East et al., 2009).

However, this social structure between related bears does not seem to be constant. In 2010, 2011 and 2012, when the most GPS data was collected from bears, the values show a fluctuation in the positive relationship. It seems that other factors from outside play an important role whether the home ranges of the brown bear, overlap more or less. A major factor could be environmental influences, such as the food resources. Most of the food resources are not distributed uniformly, but in patches (Begon et al., 2006). This could lead to more interactions and overlaps of home ranges of brown bears. The more profitable the year is for the bears' food intake, the higher the values should correlate with each other. This could indicate that social structure we are observing here is a spatial-social structure.

When analyzing the two areas separately, the correlation between kinship and overlap was stronger in Eastern Finland than in central Finland. However, this result was not statistically significant and further data would be necessary for the correlation. Bear density is known to be higher in eastern Finland than in central Finland (Kojola and Heikkinen, 2006). Perhaps it is the high density of bears that makes bears more willing to share their home range and resources with closer related bears (Schenk et al., 1998). This would also confirm a spatial-social structure in bears.

Brown bears are mostly living solitary. However, the positive relationship between the degree of relationship and the overlap of the home ranges has shown that they live in social structures. This social structure can be described as a form of a socio-spatial organization in brown bears of Finland. This mean in conclusion that bears do have a social structure and are social animals. Social interaction can vary greatly between large carnivores and the social structure of a group living carnivore is not the same as the social structure of a solitary animal

(McLellan and Hovey, 2001). But the results indicate that social structures may be more present in solitary species than previously assumed (Ordiz et al., 2008).

5 Perspective

The brown bear (*Ursus arctos*) is a well-studied species, as several publications have shown (Steyaert et al., 2012; Taberlet et al., 1995). Nevertheless, there is no reason to reduce the research on brown bears and here are several reasons for this: 1. With the increasing human population, the problems with large carnivores will increase (Kojola and Heikkinen, 2012). The amount of overlaps of bears' home ranges with human settlements will rise. Contact with humans will increase also due to the increasing wildlife tourism’s in Finland (Figure 23) (Kojola and Heikkinen, 2012). Consequences of the overlap can have an impact on their social structures. In addition, in the form of deforestation for new residential and commercial areas, living areas are going to be reduced and fragmented for bears. Herby the consequences might be changes in the size of the home ranges and gene flow between populations. 2. The in-depth research into the social structures of the bear would not only serves to protect and manage the wildlife of the bear species itself, but also an entire ecosystem (Schwartz et al., 2003). The brown bear, compared to other living animals, is perceived more in the social human environment (Clucas et al., 2008). It create a certain fascination but also fear to humans (Linnell et al., 2000). It not only occurs in the old stories of the Sami people, but also in today´s children book stories or TV series (Surojegin, 1999). This fact makes the bear a flagship species. Flagship species are popular, charismatic species animals that can symbolically represent an entire ecosystem for conservation issues (Heywood, 1995; Simberloff, 1998). The protection and attention that can be obtained through research on the Finnish brown bear would not only improve the situation of the brown bears in Finland and secure them for the future, but also for several other species that share the same ecosystem with the bear population.

Figure 23: Photograph of an observation stations for tourists to observe wild brown bears that are attracted with supplementary food (upper photography) and bear family that is attracted to the feeding place (lower photography) (by Seppo Kemppainen).

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6 Summary

The brown bear (*Ursus arctos*) is the largest carnivore living in Europe, is well represented in Finland with approx. 2000 individuals and is not in danger of extinction according to the annual census size estimation which is done by Luke (Natural Resource Institute Finland). However, this has not always been the case. At the beginning of the 20th century, the bear population in Finland was drastically reduced, mainly due to illegal bear killing such as hunting or to reindeer herder protecting reindeers in the north. After legal protection of bear started in the middle of the 20th century and closer monitoring of the bear population was established, there was increase in the bear population in Finland. Many bears have immigrated from the eastern Russia (mainly Karelia). Nowadays the bear population is mainly focused on the east, near the Russian border and in the central part of Finland.

The aim of this master thesis is to evaluate the social structure of the solitary living brown bear. The social structure was studied analyzing the relatedness of the brown bears and the overlap of the individual home ranges. It is believed that the higher the degree of kinship is, the more the home ranges of brown bears overlap. We measured the relatedness in two areas: In Eastern and Central Finland in order to study if there is difference in the social structure of brown bear between these two areas: We also used GPS coordinates from radio collared brown bears in order to calculate their home range size and the percentage of overlaps. A total number of 119 samples has been analyzed for their degree of genetic relationship. Furthermore, out of 119, 53 bears were marked with GPS collars.

According to the results the female's brown bears are in Central Finland more closely related to each other than females in Eastern Finland. Male bears did not show the same significant relatedness difference between the two regions. One possible explanation might be that in eastern Finland a higher number of migrations can be observed between the Russian Karelian brown bear population and the eastern brown bear population. This leads to a higher gene flow and a higher density of brown bears in that area and less relatedness. Subadult male brown bears tends to disperse from natal area in order to find mates and to reduce the probability of inbreeding. This fact might be the reason that there was no difference in relatedness in males in the two regions.

In average the female home range was significantly smaller than in male brown bears in both regions. Also, the female home range in Eastern Finland was significantly smaller than the home ranges of female brown bears in Central Finland. The size of the home range of brown bears is influenced by several characteristics such as habitat quality, density and for female reproductivity. High food availability and high bear density lead to the fact that brown dears decrease their home range. In order to avoid infanticide of cubs, female bears try to protect their offspring against male brown bears by reducing contact with other brown bears and reducing home ranges.

A slightly positive correlation was detected among the relatedness and the degree of home range overlaps. The more closely the brown bears are related to each other the more home range overlaps were detected. These results can be explained by the fact that brown bears tend to be more social animals than expected. In order to increase their reproductive fitness brown bear mother´s, seem the accept home range overlap with a female offspring. With this social behavior she increases the probability that her offspring will survive successfully and on the other hand her own home range is better protected from other dominant and non-related females. Dominant females are usually older brown bears, so that it seems that age structure has also some influence for this social organization. This social interaction seems to be fluid and is not constant over years. Home ranges are strongly depended on habitat quality and reproduction status of the dominant female. Good food availability increases the acceptance in bears to overlap home ranges. Females that do not have a cup seem also roam to mate as males and thus to increase the home range overlaps.

Monitoring the social behavior of brown bears is recommended as the future will challenge large carnivores with new problems such as an increasing number of human settlements´ along with more fragmented areas because of infrastructure and increasing wild animal tourism in Finland.

7 Acknowledgments

I would like to thank the people who contributed significantly to the creation of this master thesis and made sure that I felt well supported during the whole time. My first thanks go to my both supervisors MSc. Jenni Harmoinen and Dr. Alina Niskanen, who supported me very well and were always available for all my questions. Furthermore, I would like to thank Prof. Jouni Aspi for the great support in all biological and administrative matters concerning my master thesis. Also, as the head of the department and of the research group “Wildlife genomics”, he made it possible for me to write my master thesis in his research group. I would also like to express my thanks to Prof. Ilpo Kojola (Luke) who, ensured that I could get all the necessary material for my master thesis. Likewise, I have to thank Vesa Nivala (Luke), because without him, I would not learnt so much about the geographical computer-based tool (ArcGIS) and my kernel creations would not have started as easily. Other thanks go to my two grants received from Societas pro Fauna et Flora Fennica and SUOMEN RIISTANHOITO-Säätiö. Last but not least, all my thanks go to the entire research group, who made the time in the lab but also in the regular meetings with them very inspiring and supportive for me.

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