DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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EGLE TAMMELEHT

Brown bear (*Ursus arctos*) population structure, demographic processes and variations in diet in northern Eurasia

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LIST OF ORIGINAL PUBLICATIONS

This thesis is a summary of the following papers, which are referred to in the text by their Roman numerals. All published papers are reprinted here with permission from the copyright owners.

I. **Tammeleht, E.**, Remm, J., Korsten, M., Davison, J., Tumanov, I., Saveljev, A., Männil, P., Kojola, I., Saarma, U. 2010. Genetic structure in large, continuous mammal populations: the example of brown bears in north-western Eurasia. Molecular Ecology 19(24), 5359–5370.

II. **Tammeleht, E.**, Remm, J., Anijalg, P., Davison, J., Keis, M., Tumanov, I.L., Kojola, I., Saveljev, A.P., Lyapunova, E.A., Vorobiev, A.A., Markov, N.I., Andersone-Lilley, Z., Ozolins, J., Abramov, A.V., Männil, P., Valdmann, H., Pazhetnov, S.V., Pazhetnov, V.S., Rõkov, A.M., Saarma, U. 2011. The brown bear population in northern Eurasia is highly structured in the west and less so in the east, reflecting the intensity of human impact. Manuscript.

III. Korsten, M., Ho, Y.W.S., Davison, J., Pähn, B., **Vulla, E.***, Roht, M., Tumanov, I., Kojola, I., Andersone-Lilley, Z., Ozolins, J., Pilot, M., Mertzanis, Y., Giannakopoulos, A., Vorobiev, A., Markov, N., Saveljev, A., Lyapunova, E., Abramov, A., Männil, P., Valdmann, H., Pazetnov, S., Pazetnov, V., Rõkov, A., Saarma, U. 2009. Sudden expansion of a single brown bear maternal lineage across northern continental Eurasia after the last ice age: a general demographic model for mammals? Molecular Ecology 18(9), 1963–1979.

IV. **Vulla, E.***, Hobson, K.A., Korsten, M., Leht, M., Martin, A.J., Lind, A., Männil, P., Valdmann, H., Saarma, U. 2009. Carnivory is positively correlated with latitude among omnivorous mammals: evidence from brown bears, badgers and pine martens. Annales Zoologici Fennici 46, 395–415.

* – maiden name

My personal contribution to the articles referred to in the thesis is as follows:

I and **II** – participation in material collection, genetic analyses, data analyses and in the writing of the article.

III – participation in material collection and in laboratory analyses.

IV – participation in material collection, scat and stomach content analyses, data analyses and writing of the article.

1. INTRODUCTION

In the vast Holarctic region, a myriad of studies on the population genetics and phylogeography of different mammal species have been conducted (e.g. Paetkau *et al.* 1999, Tomasik & Cook 2005, Aspi *et al.* 2006, Hoffman *et al.* 2006, Charlier *et al.* 2007, Williams & Scribner 2010, Mucci *et al.* 2010). The brown bear is one of the best studied non-human mammal species in this respect; it has been the subject of many genetic studies in Eurasia (Taberlet & Bouvet 1994, Kohn *et al.* 1995, Waits *et al.* 2000, Manel *et al.* 2004, Lorenzini *et al.* 2004, Saarma *et al.* 2007, Saarma & Kojola 2007, Zachos *et al.* 2008, Kruckenhauser *et al.* 2009, Murtskhvaladze *et al.* 2010) and North-America (Paetkau *et al.* 1998a, Paetkau *et al.* 1998b, Proctor *et al.* 2005, Cronin *et al.* 2005), and is consequently treated as a 'model species'. Nonetheless, there remains a striking lack of knowledge concerning the genetic structure of the brown bear population in northern continental Eurasia, which comprises the largest part of the species range (Chestin 1999). An important reason for this might be the relatively low interest of conservation biologists and wildlife managers in this apparently large, unthreatened population, since most studies have been centred around conservation efforts (summarised in Swenson *et al.* 2011). However, reductions in bear numbers due to habitat destruction, extensive hunting and poaching (Chestin *et al.* 1992, Revenko 1995) have also been documented in large parts of the Russian bear distribution. Hence, the population structure and gene flow between population genetic groups in the northern continental Eurasian brown bear population are of relevance to conservation and management, especially considering the time lag between changes in population trends and the public reaction to them (Swenson & Sandegren 1996). At the same time, this still continuous and numerous population has great potential to provide information about the formation and maintenance of genetic structure in widespread wild mammal populations.

More than a half of the existing European brown bear populations (together 12 populations, according to Zedrosser *et al.* 2001) are small with populations numbering fewer than 500 individuals. Among the larger populations, four have a population density higher than 15 individuals per 1000 km^2 of distribution area (Zedrosser *et al.* 2001). Several of these small populations are the result of recent reintroduction programs, while the naturally continuous populations have all undergone one or more population bottlenecks during recent centuries. The status of brown bear populations has also varied considerably throughout north-eastern Europe (Estonia and Finland) and central and northern Russia, which constitutes the main study area considered in this thesis; although before of the 1800s brown bears are believed to have been numerous throughout the entire area (Chestin *et al.* 1992, Pulliainen 1972, Kaal 1974). The population in Finland started to decline in the 1800s – initially in the south-western and southern parts of the country (Pulliainen 1972) – and reached its lowest point during the early decades of the 20th century (Nyholm & Nyholm, 1999), when it was restricted to a narrow range in the north and east of the country (Pulliainen

1972). From the 1920s, the population started to increase, reaching 150–200 individuals by the 1970s (Pulliainen 1972), 430–600 by the 1990s and around 900 individuals in recent years (Wikman 2009). A similar situation has occurred in Estonia, with a decrease in the 1800s culminating in population low in 1900–1920, when about 10 bears were estimated to live in Estonia, followed by a subsequent increase (Kaal 1974). By the beginning of the1970s there were about 150 brown bears in Estonia, separated into two small populations: one in north-eastern Estonia (consisting of about 90% of population); and the remaining brown bears in south-central Estonia (Kaal 1974). The north-eastern population was assumed to share migrants with brown bears from Leningrad oblast, and Kaal (1974) predicted separation between these populations due to the growth of the oil-shale industry in north-eastern Estonia and argued that such scenario would endanger the Estonian population because of the potential for inbreeding. Brown bear numbers in the 1990s in Estonia have been estimated at 200–600 individuals (Valdmann et al. 2001), and the current official estimate is about 700 individuals. A decrease in Russian bear populations occurred in the 1960s (Chestin et al. 1992), later than in Estonia and Finland, and its subsequent increase is believed to have been a source of the population increase in Finland in the 1970s and 1980s (Pulliainen 1990) due to immigration. The peak in Russian brown bear numbers was in the 1990s (Chestin 1999), by which time the brown bear population in the Volga federal district had doubled since the low point, while in the Northwestern and Far Eastern federal districts the increase has continued until now albeit only slightly (Kolesnikov 2009). Brown bear numbers have decreased in the Central, Urals and Siberian federal districts (Kolesnikov 2009) since the 1990s; nonetheless, the estimated total brown bear population in Russia contained about 10 000 more animals in 2008 (133 980 individuals) than in the 1990s (123 869 individuals) (Chestin 1999, Kolesnikov 2009).

Three subspecies of brown bear are believed to occur in the area of northern continental Eurasia: *Ursus arctos arctos* (inhabiting an area from Western-Europe to the Yenisey river and Altay mountains), *U. a. yeniseensis* (from the Yenisey river to the Lena and Kolyma rivers) and *U. a. piscator* (on the Kamchatka Peninsula and possibly the Chukotka Peninsula and the coast of the Okhotskoye Sea) (Geptner *et al.* 1967). These subspecies differ not only in their morphology, but also in ecological characteristics, including habitat associations and diet (Chestin *et al.* 1992). However, brown bear taxonomy is problematic, and there is reason to believe that these morphological and ecological subspecies represent are genetically distinct groups. It is notable that the results of a population genetic study in Alaska did not detect any substantial genetic isolation between the putative subspecies in that area: the large brown bears of coastal Alaska and British Columbia, and the smaller brown bears of the interior (*U. a. dalli* and *U. a. horribilis*, respectively) (Paetkau *et al.* 1998b). Even if the question of subspecific denomination has limitations, ecological characteristics might still cause populations substructuring even if genetic isolation is not as great as might be the case with subspecies (i.e. morphological differentiation has taken place before the genetic). Although brown bears are adaptable omnivores, their dispersal to new ranges is largely limited by the distribution and availability of dietary items (McLoughlin *et al*. 2000, Merill *et al*. 1999). The availability of dietary items played an important role in the colonization of suitable areas after the retreat of ice cover following the last ice-age.

Three basic marker systems are available for genetic studies: 1) uniparental mitochondrial DNA (mtDNA), which characterizes maternal lineages, 2) biparental autosomal markers such as microsatellites, which characterize the combined history of female and male lineages, 3) and uniparental sex chromosome markers, like Y-chromosome microsatellites, which characterize paternal lineages. Most phylogeographic studies have been based on analysis of mtDNA for several reasons. The advantages of mtDNA are: it is present in cells in high copy number, it does not usually recombine, it has relatively rapid mutation and coalescence times, and it is maternally inherited. The final point makes mtDNA particularly useful for studying species, like the brown bear, where females are more philopatric than males (McLellan & Hovey 2001, Støen *et al*. 2006). This is because in such species geographic structure in mtDNA is likely to change more slowly than that in autosomal markers, and hence is more likely to preserve the signatures of phylogeographic processes. Microsatellites are short tandem repeats, in which differences in allele length can arise due to replication slippage. Microsatellites have been a very useful tool in population genetic studies because they are neutral, codominant, biparentally inherited and fairly abundant and well-dispersed throughout the genome (Tautz *et al*. 1986, Weber & May 1989). The mutation rate in microsatellites is relatively high (Dallas 1992), which makes them highly variable, and thus suitable for detecting relatively subtle differences between populations and subpopulations. These two markers – mtDNA and microsatellites – have been widely used in studies of phylogeography and population genetics, including those on brown bears (e.g. studies using mtDNA: Taberlet & Bouvet 1994, Waits *et al*. 1998, Miller *et al.* 2006, Saarma *et al*. 2007, Valdiosera *et al*. 2007; studies using microsatellites: Paetkau *et al.* 1998a, Waits *et al*. 2000, Manel *et al*. 2004, Kruckenhauser *et al*. 2009). We also considered these to be the most suitable markers available for our study.

Four major mitochondrial clades have been identified among modern brown bears, and subclades defined within three of these (Talbot & Shields 1996, Waits *et al*. 1998, Randi *et al*. 1994, Taberlet & Bouvet 1994, Kohn *et al*. 1995, Saarma *et al*. 2007, Murtskhvaladze *et al*. 2010, Matsuhashi *et al*. 1999). Within Eurasia, subclade 1a is found in southern Scandinavia, Spain and France; subclade 1b in the south and south-east of Europe; subclade 3a in the north-east and east of Europe and the north of continental Asia and Japan; and subclades 3b and 4 in Japan. In continental Eurasia population genetic studies have mainly been restricted to a handful of European populations (reviewed in Swenson *et al*. 2011). However, these studies have been performed on local populations, while studies on a wider scale and data from the North-Eastern European population (as defined by Zedrosser *et al*. 2001) are lacking.

Diet has been one of the most crucial factors determining historical brown bear movements in response to significant environmental changes such as long term climatic variations (i.e. ice-ages). The composition and availability of suitable sources of food affects habitat use (Nomura & Higashi 2000), productivity (Hildebrand *et al.* 1999) and the spatial structure of populations (McLoughlin *et al.* 2000). Several studies on brown bear diet have been conducted in Europe, including populations that are representative of much of the distribution area: from Spain in south and west, to Croatia in east, and Norway in north (Naves *et al.* 2006, Cicnjak *et al.* 1987, Persson *et al.* 2001). Although broad food item groups are similar everywhere (e.g. vegetative plant material, fruits/berries, insects, mammals), the specific composition of brown bear diet varies between regions depending the distribution of different dietary species. Several diet studies have also been conducted in the Russian part of northern continental Eurasia (e.g. Akhremenko & Sedalishchev 2008, Vaisfeld & Chestin 1993, Pazhetnov 1990), but unfortunately the methods used in these studies prevent reasonable comparisons to be made. However, taking a coarse view of diet composition, it is known that unlike bears in Europe, bears in the Russian Far East eat a lot of fish (mostly different salmonid species) and in some areas of Siberia, e.g. in Krasnoyarski krai, Khabarovsk and the Baikal region, the main food of bears in autumn is Siberian pine nuts, whereas in Europe it is mostly berries. As nuts are even the sole autumn food source for some Far Eastern populations, reproductive success declines and mortality rate increases after years of low nut yield (the population size was reduced by 67%) (Chestin 1999).

The main goal of this thesis is to investigate brown bear population genetic structure in northern continental Eurasia, and analyse latitudinal variation in brown bear diet. To achieve these aims, 1) biparental genetic markers were used to assess the genetic structure and population processes among brown bears in northern continental Eurasia, 2) the role of maternal lineages and important phylogeographic processes in Eurasia were investigated using mitochondrial DNA, 3) brown bear dietary analysis was conducted in Estonia, and these results were compared with those obtained in earlier studies of brown bear diet in Europe in order to assess latitudinal variation in bear diet in Europe.

2. MATERIALS AND METHODS

2.1. Data collection

2.1.1. Samples for DNA analyses

Muscle, liver and hair samples from 337 brown bears were collected across northern continental Eurasia for DNA analyses (**I–III**); subsets of 193 samples (**I**) and 294 samples (**II**) were used for microsatellite analyses and a subset of 205 samples was used for mtDNA analyse (**III**). Samples were collected in 1996–2007 from Estonia, Finland and different regions of Russia as represented in Fig. 3 in **III**, Fig.1 in **I** and Fig.1 in **II**. Muscle and liver samples were stored in 96% ethanol at –20°C prior to the extraction of genomic DNA. Hair samples were dried and stored in paper envelopes. Total genomic DNA was extracted using the QIAamp DNA Mini Kit (Qiagen) or the High Pure PCR Template Preparation Kit (Roche Diagnostics), following the manufacturer's protocols.

2.1.2. Samples for dietary analyses

A total of 142 scats and 12 stomachs were collected in 2003–2004 from the core area of the Estonian brown bear population (see study area in Fig.1 in **IV**) for bear dietary content analyses. Scats and stomachs were kept frozen at –20°C until further analysis.

Data from six earlier studies in other regions in Europe (Appendix 1 in **IV**) that applied similar analytical methods and seasonal subdivision were used for analyses of latitudinal variation in the brown bear diet in conjunction with data from **IV**. If not given in the original sources, estimates of total consumption of plant and animal food were calculated as arithmetic means.

Hair samples for stable isotope analyses were collected using a standard semi-invasive DNA hair-sampling method (n=29; Woods *et al.* 1996, Mowat & Strobeck 2000) at 37 sites in the study area during 2000–2004 and from trophy furs (n=10) collected within the study area in 1999–2004. Each hair-trapping site consisted of an approximately 30-m perimeter fence of single-strand barbed wire placed 0.5 m above the ground and an elevated bait of cattle blood and/or rotten meat inside the perimeter (Woods *et al.* 1996). Sampling sites were visited 7 and 14 days after set up to remove hair samples. Reference samples for stable isotope analysis were taken from the main components of brown bear diet as listed in **IV**.

2.2. Laboratory analyses

2.2.1. Genotyping and sequencing

Microsatellite genotyping for articles **I** and **II** was performed on 17 loci using primer pairs previously described in the literature: Cxx20 (Ostrander *et al.* 1993), G10J, G10O (Paetkau & Stroebeck 1994), G10B, G10C, G10D, G10P, G10X (Paetkau *et al.* 1995), G10L, Mu10, Mu23, Mu50, Mu51, Mu59 (Bellemain & Taberlet 2004), G1A, G10H, Mu15 and SRY (a Y-chromosome locus for gender determination) (Taberlet *et al.* 1997). For article **III** 1953 base pairs (bp) of mtDNA was sequenced: the full cytochrome b sequence (1140 bp), the 5' and middle sections of the control region (664 bp) and sequences (149 bp) flanking the cytochrome b gene and control region. Reaction conditions can be found in the Materials and Methods of articles **I-II** (for the PCR conditions in microsatellite analysis) and **III** (for the PCR conditions, shrimp alkaline phosphatase and exonuclease I treatment and cycle sequencing reaction for mtDNA analysis) at the end of this dissertation. Amplified products for microsatellite analyses (**I** and **II**) were diluted in distilled water (20x dilution, except 10x dilution for G10P) and separated on an ABI 3130xl automated sequencer (Applied Biosystems) in four capillaries as described in **I**. Sequences of mtDNA were resolved on ABI PRISM 377 or 3130xl automated sequencers (Applied Biosystems). For fragment sizing in articles **I** and **II**, a GeneScan 500 LIZ size standard (Applied Biosystems) was used and microsatellite alleles were sized and genotyped with GeneMapper v4.0 (Applied Biosystems).

2.2.2. Dietary analyses

Scat and stomach content analyses for article **IV** followed the methodology described by Hamer and Herrero (1987). Scats and stomach contents were washed through a 0.8 mm mesh. Five 6-ml wet subsamples were taken from the homogenous remains for content analyses. All food items were identified to the lowest taxonomic level possible using a microscope. Food items were separated from each other and their proportion in the sample was visually estimated as described by Mattson *et al.* (1991). Trash (twigs, wire, stones, wood fragments, etc.) was ignored in further analyses as items with very low nutritional content.

Bear hair samples were cleaned with a 2:1 chloroform-methanol solution and dried under a fumehood for stable isotope analysis (**IV**). Plant material was cleaned with distilled water, dried at 60 ºC and powdered with a mechanical grinder. Animal samples were dried, and lipids removed by rinsing in a chloroform-methanol solution. Subsamples of approx. 1 mg were loaded into tin cups and analysed with a Europa 20:20 continuous flow mass spectrometer interfaced with a Robo-Prep elemental analyzer. Stable isotope measurements were expressed in standard delta notation relative to Vienna Pee Dee Belemnite (VPDB) and atmospheric air (AIR) for $\delta^{13}C$ and $\delta^{15}N$, respectively. For hair and tissue samples, egg albumen was used as a working laboratory standard and was measured between every five samples in a sequence. This standard was replaced by a peagrain laboratory standard when analysing plant material. Analytical error was estimated to be ±0.1‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$ measurements, based on the laboratory standards.

2.3. Statistical analyses

2.3.1. Population genetic analyses

Descriptive statistics (Table 1 in **I** and in **II**) were calculated with Excel Microsatellite Toolkit (Park 2001) and Fstat v.2.9.3 (Goudet 2001). Genetic differentiation indices between sampling sites (Table 2 in **I**) and clusters (Table 4 in **I**) were estimated using Arlequin 3.11 (Excoffier *et al.* 2005; for F_{ST}) and Doh (for D_{LR}; Paetkau *et al.*1997).

The Bayesian method of Pritchard *et al.* (2000) and Falush *et al.* (2003) was used to detect genetic clusters: the program Structure v.2.3.1 and v.2.3.3 were used for cluster analyses in article **I** and **II**, respectively. The parameters used to run Structure can be found in Material and Methods sections of articles **I** and **II** at the end of this dissertation. The numbers of clusters were estimated using the method of Evanno *et al.* (2005). In addition to the Bayesian method, factorial correspondence analysis, implemented in Genetix 4.05.2 (Belkhir *et al.* 1996–2004) was used to detect and visualize structural relationships in data (II).

Isolation-by-distance (IBD) analyses in article **I** included 177 bear samples, whose sampling locations were precise to <200 km. D_{LR} between all pairs of these samples was used as a measure of genetic distance. Pairwise non-linear regression was used to determine the maximum distance at which genetic similarity between samples was dependent on geographical distance (IBD range). The regression fit was compared with a null-model constructed in 33-km-wide increments, and 95% confidence intervals were estimated using 1000 bootstrap iterations.

The locations of possible subpopulation core areas and transitional areas in **I** were also estimated spatially using D_{LR} values. The R package Gstats (Pebesma & Wesseling 1998) was used to model spatial autocorrelation in mean of residual D_{LR} using the variogram method. The spatial distribution of mean residual D_{LR} was interpolated over the entire studied area using ordinary kriging.

2.3.2. Phylogenetic analyses

Consensus sequences of mtDNA for article **III** were generated using Consed (Gordon *et al.* 1998), aligned using ClustalW (Thompson *et al.* 1994) and checked and corrected in BioEdit (Hill 1999).

Median joining networks were calculated using Network 4.500 (Bandelt *et al.* 1999). Two different network analyses were performed for article **III**: 1) based on full cytochrome b sequences (1140 bp) from all bears sequenced in this study and additional sequences from GenBank; 2) based on full cytochrome b, partial control region, and flanking region sequences (in total, 1942 bp) from all bears sequenced in this study. The hypervariable pyrimidine tract (10bp) of the control region was excluded from network analyses due to its high level of homoplasy. Based on microsatellite data, a neighbour-joining phylogenetic tree was generated with TreeToy (available at http://www2.biology.ualberta.ca/jbrzuto/TreeToy.php) to reveal evolutionary relationships of five genetic clusters (**II**).

Bayesian phylogenetic estimates of divergence times were calculated using HKY and HKY+G substitution models in BEAST 1.4.7. (Drummond & Rambaut 2007), assuming an uncorrelated log-normal relaxed-clock model. The shape parameter (alpha) of the gamma distribution for rates across sites was estimated at 0.269, with a 95% highest posterior density interval of 0.188–0.358. Posterior distributions of parameters were estimated by Markov Chain Monte Carlo sampling.

Measures of genetic polymorphism and demographic expansion (Table 3 in **III**) were calculated using DnaSP v. 4.5.03. The significance of tests was determined using 1000 coalescent simulations without recombination.

2.3.3. Dietary analyses

Frequency of occurrence (FO, %) and proportional volume (FV, %) of each diet item were calculated in article **IV** as in Dahle *et al.* (1998). To estimate the dietary content (EDC, %) and the total energy content (EDEC, %), respective correction factors were used as given in the literature (Hewitt & Robbins 1996, Johansen 1997, Dahle *et al.* 1998, Swenson *et al.* 1999, Persson *et al.* 2001). Correction factor values can be found in the Material and Methods section of article **IV**. All statistical tests were performed using STATISTICA 8.0 (StatSoft, Inc.).

To gain an insight into the relative contributions of potential dietary items to bear during the period of hair grow, we used bear hair stabile isotope values and the stable isotope values of reference samples in isosource mixing model (Phillips 2001). Equations relating bear plasma to diet, derived by Felicetti *et al.* (2003) for bears raised in captivity on known diets ranging from fruits to meat, were used, because discrimination values calculated for bear plasma are the same as those for hair (Hildebrand *et al.* 1996).

3. RESULTS

3.1. Genetic structure of brown bear populations in Eurasia

Clustering analysis of the microsatellite dataset from the European part of our study area (**I**) identified two major clusters. However, the analysis also revealed a lower peak in likelihood values for K = 4, indicating probable substructure with 4 genetic groups (Fig. 3 in **I**). Therefore, we reanalysed both major clusters individually as suggested by the authors of Structure (Pritchard & Wen 2004). Reanalysis of Cluster 1, which mostly consisted of Estonian samples, did not reveal any subdivision. Reanalysis using samples from the very large second cluster (n = 130: all bears, except Estonia,) suggested the existence of three genetic subgroups (Fig. 3B in **I**). Samples mainly from Kirov, Arkhangelsk and northern Finland formed one cluster, while the other two clusters consisted mainly of samples from southern Finland and western Russia (Leningrad oblast), respectively (Fig. 1A in **I**). The addition of 106 further samples from Estonia (n=12), Kirov oblast (n=1), Siberia (n=40), Far East (n=6) and Kamchatka peninsula (n=42) to this dataset (**II**) identified an additional cluster with a wide distribution, including bears from Eastern Siberia, the Far East and Kamchatka (n=53). Moreover, the span of the largest cluster in study **I** was found to be much wider, extending from northern Finland through Kirov oblast to Western Siberia (consisting of Perm, Sverdlovsk and Novosibirsk oblasts). Defining cluster borders as the distribution of individuals with > 50% of membership coefficient (MC) to respective cluster of belonging to a the cluster revealed a pattern of considerably overlapping clusters; however if only individuals with very high cluster membership probabilities (> 95% MC) are considered, the five clusters were non-overlapping with distinct geographic limits. No sharp geographical borders were between these clusters. Among the sampling locations, highest membership coefficient of samples belong to a particular cluster was in Estonia and Kamchatka (Table 3 in **II**). All genetic groups were significantly distinct from others by fixation index values and genotype likelihood ratio distances (Table 2 in **I** and Table 2 in **II**). Highest genetic diversity was found in the clusters covering the largest areas: the northern Finland – western Siberia subcluster and the eastern Siberia – Kamchatka cluster (Table 1 in **II**). Lowest genetic diversity was found in the Estonian cluster (**I**, **II**). The IBD range extended up to ~350 km (Fig.2 in **I**).

Based on mitochondrial cytochrome b sequences (1140 bp), brown bears in northern continental Eurasia were divided in network analysis into two haplogroups: Eurasian and Kamchatkan (**III**). Within the Eurasian haplogroup, more than 60% of analysed bears belong to a single haplotype (E1), which was found throughout northern continental Eurasia (Fig. 1A in **III**). There were two haplotypes geographically restricted to Estonia and neighbouring districts of Russia, and one haplotype was restricted to Finland and European Russia. The Kamchatkan haplogroup consisted solely of bears from Kamchatka Peninsula, although two haplotypes from the Eurasian haplogroup were also found in Kamchatka. Based on the 1942 bp dataset, four haplogroups appeared: widely distributed haplogroups (EA and EB), and haplogroups specific to Estonia (EC) and to Kamchatka (KA) (Fig. 3 in **III**). All statistics yielded results consistent with population expansion at the levels of the whole data set (Table 3 in **III**). Estimates of demographic parameters in the Bayesian analysis revealed also evidence of significant population growth in brown bears. The age of the most recent common ancestor (MRCA) of brown bears was estimated to be 193 000 years (with a 95% highest posterior density interval of 114 00 – 325 000 years) (Table 4 in **III**).

3.2. Diet and its geographical variation

Identification of the remains of digested food items recorded 104 taxa as brown bear food items in Estonia (Appendix 3 in **IV**). Different vegetative plant items were most frequent among food items: plants occurred in almost 97% of analysed scats, providing almost 44% of yearly estimated dietary energy content (EDEC). Although animal food items were less frequently consumed (59%), they provided over the half (53.5%) of the yearly EDEC (Table 1 in **IV**). Although in spring and summer animal items contributed more to EDEC (52.9% and 8.3% from mammals and insects in spring, respectively, and 56.6 % and 27.6% from mammals and insects in summer, respectively), in autumn most of digested energy originated from plants, such as cereals (53.2% EDEC), berries (19.3 % EDEC) and apples (10.6% EDEC) (Table 2 in **IV**).

According to the Isosource mixing model, insects had the highest mean contribution (41.9%) to brown bear diet in Estonia during the hair growth period (late summer-autumn), while graminoids, forbs and berries contributed 10–20% (Table 5 in **IV**). A dual-isotope multisource-mixing polygon, representing the solution space for the Isosource model used to estimate the relative contributions of various categories of food items can be found in Fig. 3 in **IV**.

Analysis of bear diet in Estonia in conjunction with similar data from six other studies elsewhere in Europe revealed a latitudinal gradient: the total proportion of animal food items in brown bear diet was positively correlated with latitude (r_s=0.91, p=0.004) (Fig.5 in **IV**). Although there was no significant correlation between latitude and diet in autumn, the correlation was significant in spring and in summer. Variation in the proportion of different plant items consumed (e.g. graminoids, forbs, berries, cereals, fruits and hard mast) differed most clearly between countries in spring and summer, with least variation in autumn, when bears eat a lot of carbohydrate-rich plant items and vegetative items (graminoids and forbs) throughout the studied range. Among carbohydrate-rich items, berries were used more in northern areas (Fig 6 in **IV**). Among animal dietary items, the consumption of mammals varied more between areas than the consumption of insects, which varied most in summer.

4. DISCUSSION

Large-scale studies on population structuring and -processes in Eurasian mammals and other animals are still rare. There are several reasons for this: first of all it is time-consuming and laborious (including logistically) to collect samples from all over Eurasia; secondly, animals that are rare in some regions in Eurasia and have been the subject of local conservation measures (such as the brown bear), are relatively numerous in others and have not been a priority for conservation-oriented scientific studies. Nevertheless, in order to preserve small populations, it is often necessary to augment them with individuals from other areas to avoid inbreeding depression and ultimately population extinction. Indeed, the first genetic studies of brown bears in Europe where initiated in order to inform such conservation initiatives (Taberlet & Bouvet 1994; Randi et al. 1994). While in many bear-countries in Europe genetic studies of brown bear populations have been carried out to some degree, brown bear populations in European Russia and in Asia have received very little attention. Moreover, without information of populations at a wider scale it is impossible or very difficult to assess the true value of local populations.

Genetic patterns derived from nuclear (**I**) and mitochondrial (**III**) data were surprisingly concordant, as was confirmed by a Mantel test (**I**). Aspects of genetic structure in biparental microsatellite data (**I**, **II**), that were apparent in the geographical distribution of mtDNA haplogroups (**III**) are:

1. Based on microsatellite data, two widely distributed brown bear genetic groups were identified in northern Eurasia: the Finnish-Russian (cluster 4 in **I**) and Far-East clusters (**II**), whereas mtDNA data revealed haplogroups EA and EB that overlap partially with the nuclear clusters (**III**). The occurrence of closely related mtDNA haplogroups and haplotypes in a very wide distribution area (~12 000 km) suggests that the brown bear population in northern continental Eurasia underwent a sudden expansion, preceded by a severe bottleneck; this is supported also by expansion-statistics and Bayesian analysis (**III**).

2. The separate genetic group of Estonian brown bears (**I**, **II**) is distinguishable regardless of the marker type (mtDNA or nuclear data) used in analysis: both **III** and Saarma *et al*. (2007) found mitochondrial haplotypes characteristic of Estonia, two individuals with Estonian haplotypes were also found in the neighbouring part of Russia (**III**); nuclear data also separated Estonian bears from others and indicated limited gene flow between Estonia and Russia – only two individuals from the Estonian cluster were found in nearby Russia, both with mixed ancestry, and several Estonian bears also had mixed ancestry (**II**). Gene flow between Estonian and Russian populations is thus very limited, most probably due to barriers built by water bodies such as the lower course of the Velikaya river, Lake Peipsi, the Narva river and the Narva resevoir. Nevertheless, the gene flow between Russia and Estonia

seems to occur, albeit infrequently, in both directions. The Russian bear population close to the Estonian border is stable (Kolesnikov 2009), whereas the Estonian population has been slightly increasing in the last decade (Statistics Estonia 2009), which might cause migration from Estonia to Russia more likely than in opposite direction

3. According to nuclear data the Finnish brown bear population is divided into two genetic groups – southern and northern (Clusters 3 and 4, **I**) – similar to the earlier mitochondrial data that identified two similarly distributed haplogroups (Saarma & Kojola 2007). This subdivision most likely reflects the post-bottleneck demography of Finnish bears within the last century: the eastern and northern part of the current Finnish population was largely formed by immigrant bears from Russian Karelia, while the remnants of the earlier population constitute a genetically distinct southern cluster.

4. Based on mitochondrial data, several haplotypes were identified that were characteristic only of bears in Leningrad oblast (**III**), and the nuclear data also revealed a distinct genetic group specific to the same area (including most of the individuals carrying a haplotype characteristic of this region) (Cluster 2 in **I**; W-Russian cluster in **II**). Although it is not easy to explain why such a distinct genetic group might exist in Leningrad oblast, it could be due to the several lakes and rivers in the area having a sufficiently isolating effect to significantly reduce the gene flow. Moreover, large cities (e.g. Saint Petersburg, Shlisselburg, Podporoche) and highways between them could negatively affect migration of brown bears in this region (Alcantara *et al.* 2007). On the other hand, the high genetic variation in this area may be a sign of a recent immigration by bears from expanding neighbouring sub-populations.

5. Samples from the Far-East and Kamchatka are well differentiated of those in European part of Eurasia based both on nuclear (**II**) and mitochondrial data (**III**). Generally speaking, there appear to be two very large dominant brown bear genetic groups in Eurasia: one distributed in the lowlands of West Siberian Plain and areas to west of it; the other in the highlands between the Central Siberian Plateau and the Kamchatka Peninsula. Unlike the geographical pattern of maternal-lineages, nuclear data didn't detect any subdivision between samples from Kamchatka and the Far-East, either in analysis with Structure or with Genetix. This may be due to male-mediated gene flow out of an expanding Kamchatkan population (Kolesnikov 2009). However, additional sampling is clearly required to confidently identify the true number of genetic clusters (scarce sampling in Asia may not have revealed all genetic groupings), their extent, borders and gene flow between them.

Relatively high genetic diversity, measured as the number of different mitochondrial haplotypes (**III**) or allelic richness in microsatellite data (**I,II**) is not entirely unsurprising, as the populations are numerous in much of northern Eurasia (see also Swenson et al. 2011). The distinction between the Russian and Estonian and southern Finland clusters are likely to reflect recent genetic bottlenecks in these areas and post-bottleneck demography that involves population increase and expansion, though admixture has not been sufficiently intense to merge these genetic groups into one. Both the Estonian and Finnish brown bear populations went through demographic bottlenecks during the 1920s (Kaal 1974, Pulliainen 1972) and started to slowly recover from that point onwards, whereas the Russian population started to recover from its low level in population numbers in 1960s (Chestin *et al.* 1992). Consequently, immigration pressure from Russia to Estonia and Finland was probably low for much of last century, as Russian bear population density was low and there would have been an abundance of available territories in Russia. However, since the population increase in Russia, migration pressure to Estonia and southern Finland has probably increased, but remains limited due to the existing reasonably dense populations in the latter areas. However, migration towards Finland has been pronounced in the eastern and north-eastern parts of Karelia. This probably reflects the fact that in the density of bears in Finland was higher in southern than northern regions after population recovery (I. Kojola, personal communication). These different levels of admixture with the Russian population have thus left a trace in the pattern of genetic structure currently detected (**I**, **II**) with a more distinct cluster in southern Finland and more admixtured population in northern Finland. The current pattern of genetic clustering in western Eurasia is a therefore probably a consequence of demographic changes and physical barriers such as waterbodies between Estonia and Russia, and a fence along the Finnish-Russian border during much of the last century.

It is somewhat surprising that two genetic clusters towards the east of Eurasia exist over such vast territories. However, as the areas inhabited by both – but especially the further east of the two – contain very low human densities compared to those in western Eurasia, this is probably indicative of the influence that mankind can have on the number and movements of wild mammal populations. An explanation for why these two clusters have remained separate is not immediately obvious. There are several types of physical barrier that might prevent more significant admixture between these large clusters. The large river Jenissei could be a very effective barrier, and mountain ranges such as Jenissei Mountain Chain and East-Sayans in the south and the Tungusi Plateau in the north may also constitute partial or complete barriers to movement. In addition, the destruction of habitats due to industrial activity in central Siberia (Chestin *et al.* 1992) may also affect the migration of bears in some areas. In the Far East the population decrease is believed to have occurred mainly due to extensive poaching (Chestin 1999), and migration to this area from the west is perhaps less attractive than migration towards the west due to low-quality habitats.

The latitudinal gradient in the feeding habits of brown bears in central and northern Europe found during the diet analysis (**IV**) could not be explained by the population genetic structure in Eurasia found in our analyses (**I**, **II**). Population substructuring in northern continental Eurasia displays a longitudinal rather than latitudinal nature. On the other hand, the studies on diet and population substructuring conducted here are difficult to compare, as the study areas only overlapped to a certain extent. The diet composition of brown bears in Slovenia and Slovakia are fairly similar in summer (Fig. 6d in **IV**) although the two populations represent highly divergent mitochondrial clades (clades 1a and 3a); and the autumn diet of all bear populations was very similar (Fig. 6f in **IV**) irrespective of phylogenetic identity. Diet has been shown to be one of the forces driving population structure in wolves (*Canis lupus*) (Pilot *et al.* 2006, Musiani *et al.* 2007). However, unlike these prey-specialists, brown bears tend to be generalists, eating various diet items in all regions (e.g. in Estonia 104 different dietary taxa were identified in brown bear diet) (**IV**). Similarly, such ecological plasticity is probably the reason why food has little influence on dispersal in another bear species, the American black bear (*Ursus americanus*) (Rogers 1987). It has also been shown that even if food specialization occurs, it does not have great influence on the genetic structure of brown bear populations: the different food habits and great variation in body size between coastal and interior brown bears in Alaska (Hildebrand *et al.* 1999) have not caused substantial genetic isolation between these populations (Paetkau *et al.* 1998b). In any case, even if differences in regionally available food items seems not to influence current brown bear population structure, flexibility in consuming different food items probably played a supportive role in the brown bear expansions of the past (**III**). This is because dietary limitations to population expansion are smaller for generalist than dietary specialist organisms, and other human derived limitations (e.g. settlements, roads etc.) to dispersal were not present at that time.

Wider and more thorough sampling throughout Eurasia is required for more precise detection of the full spatial extent of the genetic clusters and matrilineal haplogroups revealed by this work. In addition, more informative genetic data (e.g. complete mtDNA sequences, more microsatellite loci, or SNPs) would help to complete this task. Furthermore, previously undetected genetic groups might be revealed through more intensive sampling (Fogelqvist *et al.* 2010). Indeed, addition of samples from western Eurasia in **II** compared with **I** changed the range of the S-Finland cluster (cluster 3 in **I**) considerably. Thus, the results of the studies presented in this thesis should be taken as initial insights into the general patterns of brown bear genetic structure in Eurasia. Moreover, better sampling has the potential to test in detail the influence of potential physical barriers using landscape genetics approaches (Manel *et al.* 2003), to reveal possible ecological factors, such as diet, that may underlie the formation of different genetic groups, and to identify migration routes between groups.

SUMMARY

Knowledge of population genetics and phylogeography of living organisms are important for conservation and management of species, since they provide information about species viability and integrity. There have been numerous genetic studies of brown bears in parts of the species' range to inform local management and conservation approaches, and due to the status of the brown bear as a 'model species' in phylogeographic studies. However, there is little information about brown bear genetics in the largest part of the distribution area: northern continental Eurasia. The goal of this thesis was to provide new information about the population genetics, diet and phylogeography of brown bears in this region, to describe population genetic structure and to assess the importance of historical and ecological conditions in generating and maintaining structure.

Analysis of microsatellite data revealed a genetic pattern with five geographically well differentiated genetic clusters with core areas in 1) Estonia, 2) western Russia, 3) southern Finland, 4) the Urals, and the northern and central part of European Russia, 5) Eastern-Siberia and the Far East (including the Kamchatka peninsula). Genetic diversity was relatively high in every cluster, although the highest values were found in the clusters with the widest distributions, whereas the lowest value was in Estonian cluster, which has the narrowest distribution.

Phylogenetic analysis based on mitochondrial cytochrome b sequences (1140 bp) identified two haplogroups. Further analysis with longer sequences (1942 bp) revealed two widely distributed haplogroups, and two geographically restricted haplogroups: in Estonia and on the Kamchatka peninsula. There was strong evidence in the mitochondrial data set of recent population expansion.

One hundred and four taxa were identified among the food items of brown bears in Estonia. Diet composition was not uniform among seasons and, while diet composition in spring and summer indicated that most digested energy was derived from animal sources, in autumn most energy came from carbohydrate-rich plants (cereals, berries and apples). Analysis of data from seven studies revealed a latitudinal gradient in brown bear diet: the proportion of animal food items in brown bear diet was higher in northern populations. Autumn was the only season when this correlation was not significant.

Similarities between the results of the population genetic and phylogeographic studies allow us to conclude that population structure in modern northern continental Eurasian brown bear population is not only a result of present conditions, but also contains a historical signature. There were analogous microsatellite clusters and mitochondrial haplotypes in Estonia, southern Finland and western Russia, and both marker types indicated that two large genetic groups (Finland-Russian and Far Eastern in microsatellites; mitochondrial haplogroups EA and EB) were widely distributed in Eurasia. Physical barriers, including waterbodies between Estonia and Russia, and a fence along the Finnish-Russian border, and demographic characteristics, particularly demo-

graphic bottlenecks in western Eurasia, may have helped to generate and maintain such genetic clustering.

Although we found a latitudinal gradient in brown bear diet, genetic structure appears to be rather longitudinal. So it is doubtful that diet has a large influence on the genetic structure of the contemporary brown bear population in northern Eurasia. The diet analysis suggests there are many food items in brown bear diet and none are without alternatives if the availability of a particular resource is low. More likely than diet, human influence (e.g. roads, habitat destruction, hunting) and population dynamics have played a role in the formation of genetic structure in the brown bear population of northern continental Eurasia. Understanding the precise occurrence of these factors and their impact on brown bear genetic structure in this vast area will require further research.

SUMMARY IN ESTONIAN

Pruunkaru (*Ursus arctos*) populatsiooni struktuur, demograafilised protsessid ja toitumisvariatsioonid Põhja-Euraasias

Populatsioonigeneetika ja fülogeograafia on olulised aspektid liikide ja populatsioonide kaitsks ja ohjamiseks, kuna sisaldavad informatsiooni populatsiooni ajaloo, sidususe ja elujõulisuse kohta. Pruunkarude populatsioonigeneetika ja fülogeograafia on pälvinud palju tähelepanu kogu maailmas tulenevalt liigi majandamis- ja kaitsevajadustest ning ka pruunkaru 'mudelliigi' staatuse tõttu fülogeograafias. Siiski, pruunkaru geneetikast on tema levila suurima osa kohta Põhja-Euraasia mandriosas vähe informatsiooni. Käesoleva väitekirja eesmärgiks on olukorda parandada, uurides selle piirkonna karupopulatsiooni populatsioonigeneetikat, toitumist ja fülogeograafiat, et leida, milline on sealse populatsiooni geneetiline struktuur ja toitumise eripärad ning üritada nende kujunemisele selgitust saada ajaloolistest ja klimaatilis-ökoloogilistest tingimustest.

Mikrosatelliitanalüüsi tulemusena ilmnes viie, üksteisest geograafiliselt hästi eristunud geneetilise klastri esinemine tuumik-aladega 1) Eestis, 2) Lääne-Venemaal, 3) Lõuna-Soomes, 4) Euroopa-Venemaa põhja- ja keskosast Uuraliteni ning 5) Ida-Siberist Kaug-Idani (k.a. Kamtšatka poolsaar). Kui esimesed kolm klastrit paiknesid suhteliselt piiratud territooriumidel Euraasia lääneosas, siis viimased kaks klastrit hõlmasid erakordselt suuri territooriume Euraasia idapoolsetel aladel. Selliste erinevuste põhjused peituvad tõenäoliselt suures inimtegevuse mõjus Euraasia lääneosas, kus populatsioonid on eelkõige ülekütti-mise, aga ka elupaikade hävitamise tagajärjel läbinud tugeva demograafilise “pudelikaela”. Kuigi kõigi klastrite geneetiline mitmekesisus oli suhteliselt kõrge, saadi kõrgeimad väärtused laiema levikuga klastrite puhul, kusjuures geneetiline mitmekesisus oli madalaim Eesti klastris, mis on ka kõige kitsama levikuga klaster.

Fülogeograafilised analüüsid tegid mitokondri tsütokroom b järjestuse põhjal (1140 aluspaari) kindlaks kaks haplogruppi. Edasiste analüüside käigus, kasutades pikemat järjestust (1942 aluspaari), ilmnes kahe äärmiselt laialt levinud haplogruppi ning kahe geograafiliselt piiratud haplogrupi olemasolu. Viimased olid omased Eestile ning Kamtšatka poolsaarele. Mitme erineva analüüsi tulemusena saadi kinnitust populatsiooni ekspansioonile kaugemas minevikus.

Toitumisanalüüsi tulemusena tehti karu toiduobjektidena kindlaks 104 erinevat liiki. Toidu koostis polnud aastaajati ühesugune ja, vastupidiselt kevadisele ja suvisele toidu koostisele, sügisel saadi enamik toiduga imenduvast energiast süsivesikuterikastest taimedest (teravili, marjad, õunad). Seitsme erineva uurimuse andmete analüüsimisel selgus, et karu toitumises esineb laiuskraadiline gradient: loomse toidu osakaal karu toidus kasvab põhjapoolsetes piirkondades. Sügis oli ainus aastaaeg, mil selline korrelatsioon ei olnud statistiliselt oluline.

Populatsioonigeneetiliste ja fülogeograafilise uurimuste vahelised sarnasused võimaldavad järeldada, et tänapäevase Põhja-Euraasia mandriosa pruunkarupopulatsiooni geneetiline struktuur ei ole kujunenud ainult tänapäevaste tegurite mõjul, vaid ka kaugemas minevikus toimunu tagajärjel. Analoogiliselt Eestis, Lõuna-Soomes ja Lääne-Venemaal paiknevatele klastritele, esines üksikuid väheesinevaid haplotüüpe, mis olid iseloomulikud just nende klastrite paiknemise aladele; ning vastavalt tuumaandmetel põhinevate kahele laialdase levikuga klastrile (Soome-Vene ja Kaug-Ida klastrid), leidus Euraasias ka kaks laialdase levikuga haplogruppi. Mingeid selgeid füüsilisi barjääre, mis sellise struktuuri tekitaksid, alal ei esine kui välja arvata Eesti ja Venemaa vahel olevad veekogud ning Soome ja Venemaa vahelisel piiril oleva tara, millel mõju võib olla kaasa aidanud praegu nähtava struktuuri tekkimisele neis piirkondades.

Kuigi õnnestus tuvastada laiuskraadiline gradient karu toitumises, siis geneetiline struktuur paistab olema pigem pikkuskraadiline. Seega on kaheldav, kas toitumisel on olnud oluline mõju tänapäevase Põhja-Euraasia pruunkarupopulatsiooni geneetilise struktuuri kujunemisele. Nagu toitumisanalüüsi tulemused näitavad, esineb karu toidus palju erinevaid toiduobjekte ning ükski neist pole alternatiivse asendus-toiduobjektita, mida tarbida kui esimese saadavus on madal. Geneetiliste gruppide kujunemisel mängivad tõenäolisemalt rolli inimmõju (nt. teed, elupaikade hävimine, küttimine) ja populatsiooni dünaamika. Nende tegurite ilmnemine ja nende mõju ulatus pruunkarupopulatsiooni geneetilise struktuuri kujunemisele sellel ulatuslikul alal vajab edasist uurimist.

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