
Genetics of brown bears in northern Europe

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Abstract: From the dawn of wildlife genetics, brown bears in Scandinavia have been studied using molecular genetic methods and hence have been substantial in the development of these methods, which are now the gold standard in DNA-based monitoring of many wildlife species. This chapter introduces the constantly evolving field of DNA-based assessments to monitor and to study the history of brown bears. Genetic studies enable us to understand better past processes, such as the recolonisation after the last Ice Age, and present status, such as migration, and other factors influencing brown bear populations in the north of Europe.

GENETICS AND THE DEVELOPMENT OF DNA-BASED POPULATION MONITORING

Genetics is the study of heredity and how an organism's genes are associated with the environment it is living in. The genetic variability or genetic diversity of a species and/or a population is essential for its adaptability to e.g. changing environmental conditions and therefore its viability and long-term survival (FRANKHAM 1995; 2005; LACY 1997; ALLENDORF et al. 2010). Molecular genetic methods have been crucial for the understanding of speciation and evolution as well as historical and current processes in Ursid biology and distribution. Genetic information helps us understand what may have shaped the brown bear (*Ursus arctos*) population in northern Europe and provides us with knowledge about its past as well as current status.

The development of DNA-technology has revolutionised how we monitor our natural environment and has also helped to improve our knowledge on numerous species, including brown bears. Individual brown bears, as every sexually reproducing species, differ genetically. An individual's genetic profile is unique, except for identical twins. Individuals usually differ in appearance and behaviour, however, these often-subtle differences are challenging to assess by human observers in other mammals. A genetic profile holds valuable information for deeper analyses, especially in comparison with the profiles from other bears, whether in the same region, adjacent areas, or across regional and national borders. Having precise genetic information from individual brown bears enables the assessment of genetic relatedness, which in turn allows addressing important questions concerning their management and conservation.

To obtain genetic information from an individual wild animal, a biological sample, such as tissue, blood, bones, hairs, or feces, must be collected in the field and then genetically analysed in the laboratory. In Scandinavia, brown bears are mainly monitored with the help of non-invasively collected material. Non-invasive sampling means that it is not required to directly have contact with, disturb,

or capture an animal to collect a biological sample. Instead, DNA is extracted from biological samples left in the field by the individual itself, for example, in the form of feces or hairs. Such samples are routinely collected by wildlife rangers, hunters, and also hikers (BELLEMAIN et al. 2005; KINDBERG/SWENSON 2018). Individual brown bears are then genetically “tagged” in the laboratory based on their unique DNA-profile; new individuals are identified and already known individuals are genetically “recaptured”. Especially the recapture of known individuals is crucial to obtain reliable population size estimates of brown bears. Over the last decade, DNA has become the population monitoring method of choice for wildlife management authorities in Sweden and Norway, and Finland is currently in the process of establishing the same method. Data based on non-invasive collection methods create a solid scientific foundation to estimate the population size of bears in a given area, but also provide additional highly valuable information, such as population distribution, population density, and the sex ratio, i.e. the proportion between males and females in the population, which is important to understand reproduction and the effect of hunting quotas (BISCHOF et al. 2016; 2020; KINDBERG/SWENSON 2018).

Feces and hair samples make up the largest part of biological materials collected for DNA analysis of brown bears in Scandinavia. The individuals identified, the date their sample was collected in the field, as well as their location and additional information, are stored and made accessible for the public in the Scandinavian monitoring database “Rovbase” (www.rovbase.no). Besides samples and information on brown bears, this database also contains similar information from other large carnivores collected and analysed via the same methods in Scandinavia (see e.g. TABERLET et al. 1999; SCHWARTZ et al. 2007). The Scandinavian brown bear was the main model species at the dawn of molecular methods for the development, design and quality of the genetic methods used today in the population monitoring of wildlife species on a global scale (BELLEMAIN et al. 2005; KINDBERG et al. 2011; SWENSON et al. 2011). The improvement of the genetic methods is an ever-ongoing process (NORMAN et al. 2013; NORMAN/SPONG 2015; DE BARBA et al. 2017).

PHYLOGEOGRAPHY OF BROWN BEARS IN NORTHERN EUROPE

In 1994, TABERLET/BOUVET (1994) published a groundbreaking study on the phylogeography of brown bears in Europe based on mitochondrial DNA-lineages of northern European brown bears. The authors identified two different brown bear DNA-lineages, indicating that Scandinavia was re-colonised by bears from two different population refugia coming to Scandinavia from two different directions after the last glacial maximum: from the north and the south (Fig. 1a). The Quaternary cold periods of the Pleistocene (2.6 million to 11,700 years ago) generally had great influence on life in Europe. As a result of the Scandinavian Ice Sheet, flora and fauna of the Holocene, the current geological epoche (11,700 years ago to today), experienced range contractions, expansion, and sometimes also extinctions in the northern hemisphere; most species were restricted to refuge areas in the southern parts of Europe. This Ice Age is ultimately responsible for today’s composition and distribution of species in northern Europe (SIIVONEN 1982; HEWITT 1996; TABERLET et al. 1998). Once temperatures were on the rise and ice caps retreated at the end of the last glacial maximum (~22,000–17,000 years ago), animal and plant species followed the retreating ice. The leading edges of these expansion fronts can be characterised by consecutive occurrences of so-called genetic population bottlenecks. A population bottleneck describes the drastic reduction in the number of individuals in a group or population accompanied by loss of genetic variation (NEI et al. 1975). Such bottlenecks, if severe enough, can be traced back in time with modern genetic methods (HEWITT 1996). Radiocarbon-dated bone remains suggest that the brown bear was one of the earliest carnivorous mammals to re-colonise northern Europe at a comparably rapid pace, which was genetically confirmed by haplogroup data

(HEWITT 1999; 2000; SOMMER/BENECKE 2005; KORSTEN et al. 2009; DAVISON et al. 2011). Today, the brown bear still is one of the most important model species to illustrate Late Quaternary mammalian phylogeography and the application of genetic methods.

The first genetic assessment of brown bears in Europe used mitochondrial DNA (mtDNA) with the goal to identify potential conservation units, i.e. areas and populations valuable for the long-term conservation of the species (MORITZ 1994). Mitochondrial DNA is exclusively inherited from the mother to her offspring and, in contrast to nuclear DNA, stored in the mitochondrion of all cells in an eukaryotic organism's body, i.e. animal, plant and fungal organisms with cells containing nucleus and nuclear envelope. The analysis of mtDNA is the basis for the tracking of a species' phylogeography, i.e. the historic and genetic processes and patterns across large time scales that have shaped the current distribution of a species (HEWITT 1996). The mtDNA of brown bears from the northern part of Scandinavia was shown to be part of the eastern lineage or clade, which is also characteristic for bears in Russia, Romania, and Slovakia. This suggests that northern Scandinavia was re-colonised by bears from eastern Europe via Russia and Finland. The mtDNA of brown bears from the southern part of Scandinavia was characteristic of the western lineage, which suggests that southern Scandinavia was re-colonised by brown bears which had their Ice Age refugium on the Iberian Peninsula, i.e. the so-called southern clade of bears found in central and southern Europe (TABERLET/BOUVET 1994).

The striking results of this first study inspired a number of follow-up research, which highlighted that these two clades originated from two separated Quaternary refugia in the far west and east of Europe (Fig. 1a–b; cf. KOHN et al. 1995; TABERLET et al. 1995; 1998; HEWITT 1999; 2000; HOFREITER et al. 2002; SOMMER/BENECKE 2005; SAARMA et al. 2007; ZACHOS et al. 2008; KORSTEN et al. 2009; DAVISON et al. 2011; KEIS et al. 2013; XENIKOUDAKIS et al. 2015; ANIJALG et al. 2018; ERSMARK et al. 2019). Further analyses of mtDNA lineages pointed to a Carpathian refuge of the eastern lineage (Fig. 1b; cf. SOMMER/BENECKE 2005; ZACHOS et al. 2008). Also, a much higher matrilineal diversity was found in bears in Finland and northwestern Russia compared to the bottlenecked Scandinavian population. This is likely due to the connection of the Finnish and northwestern Russian population to the large and stable populations in Russia, while the Scandinavian population was likely isolated from potential immigration of new individuals from the east (SAARMA et al. 2007). A recent study challenged the scenario of the Iberian peninsula as refugial area, as the genetic analyses of historical material of bears from Belgium and France indicate that this specific haplotype may be the origin of expansion of brown bears into southern Scandinavia (ERSMARK et al. 2019).

The general conclusion is that the eastern and western genetic lineages of brown bears diverged about 0.85 million years ago and that bears re-colonised first southern Scandinavia from western Europe, followed by northern Scandinavia from eastern Europe. Here, both mtDNA-lineages possibly met about 5,000–9,000 years ago (TABERLET et al. 1995; XENIKOUDAKIS et al. 2015), after the ice shield from the last glaciation had melted (SIIVONEN 1982). The eastern and western mtDNA-lineages are highly divergent, and a follow-up study further described the delination or contact zone in the middle of Sweden, where these two clades meet. The width of the contact zone was estimated to be ~130 kilometres. At the time of the study, only four individuals were identified that have crossed the contact zone from one lineage to the other (TABERLET et al. 1995). Overall, the mtDNA-haplotype diversity especially in southern Scandinavia was higher, as the genetic analysis of historical samples of brown bears archived at Swedish museums suggested (XENIKOUDAKIS et al. 2015).

The current distribution of brown bears in Europe is shaped by centuries of severe persecution, bounty hunting, and rigorous extermination efforts (ZEDROSSER et al. 2011; ALBRECHT et al. 2017). Brown bears were also eradicated from most parts of northern Europe, and the once continuous population was split into the Scandinavian to the west and the Karelian in the east (CURRY-LINDAHL 1972; SWENSON et al. 1995). It is assumed that the population in Scandinavia at its lowest point at the

end of the 19th century was not larger than about 100 individuals (SWENSON et al. 1994). Due to the beginning of modern conservation-oriented thinking and management in the early 1970s, brown bear populations, along with other large carnivores, started to recover and to re-colonise their former distribution range in northern Europe (CHAPRON et al. 2014). However, despite regional comebacks, such as in northern Europe, brown bears and other large carnivores are still under substantial pressure and considered as endangered in Europe and other parts of the world (DALERUM et al. 2009; RIPPLE et al. 2014).

ASSESSING CONTEMPORARY STATUS BY USING NUCLEAR DNA

Shortly after the first studies of mtDNA in brown bears and other wildlife had emerged, more genetic markers as well as new techniques were developed to enable the study of diversity via nuclear genetic variation. Such studies investigate historic as well as contemporary genetic patterns by using highly variable genetic markers, such as microsatellites or short-tandem-repeats (STRs). Microsatellites have been used since the 1990s, and their application intensified until recently (PAETKAU/STROBECK 1994; PAETKAU et al. 1995; TABERLET et al. 1997). With the development of next-generation sequencing and genomics, even more informative genetic marker systems were developed, such as single-nucleotide-polymorphisms (SNPs; NORMAN et al. 2013) or restriction site-associated DNA sequencing (RADseq; ANDREWS et al. 2016). All genetic marker systems have their advantages but also shortcomings. Mitochondrial DNA, inherited from the mother, can only enable insights into female-mediated genes and gene flow. In comparison, nuclear DNA is inherited from both parents and can be applied to the study of the more recent history as well as the current status of populations in relation to genetic variation, inbreeding, population substructure, interpopulation connectivity via gene flow and more, all of which are important for conservation and management of a species (FRANKHAM 1995; 2005; WAPLES/GAGGIOTTI 2006; ALLENDORF et al. 2010). NORMAN et al. (2013) published a SNP-panel to study genetics and specifically the relatedness among individuals in Scandinavian brown bear. In contrast to the first nuclear genetic markers, the higher resolution of SNPs allows even more specific assessment of the genetic relationships among bears without prior biological information on their relatedness and family groups (NORMAN/SPONG 2015).

In 2000, the first study on brown bears in Sweden using microsatellites was published (WAITS et al. 2000). It was also the first comprehensive assessment of the brown bear's contemporary genetic variation and population structure using genetic methods in northern Europe. The results of that study showed that the genetic diversity of brown bears in Sweden was comparable to brown bear populations in North America. This was surprising, considering the drastic population decline and bottleneck Scandinavian brown bears had experienced due to the intensive hunt. The study also showed that the Swedish population appeared to be subdivided into four different subpopulations, of which the southernmost was geographically located below the previously described contact zone where the two distinct mtDNA-lineages meet (TABERLET et al. 1995). The same study was re-analysed with advanced Bayesian statistical methods a few years later, and the authors concluded that the Swedish population consisted not of four but rather of three subpopulations, with the individuals from the previously identified two northernmost subpopulation showing substantial geographical overlap, leading to the conclusion that these two subpopulations comprise of just one unit (MANEL et al. 2004), shaped by isolation-by-distance (SCHREGEL et al. 2018).

The reasons for the distinct genetic structure of brown bears in Scandinavia remained unclear until XENIKOUDAKIS et al. (2015) published a study based on the genetic analysis of archived museum samples using historical bone, skin, and tooth samples. Their findings showed that the current genetic structure is the result of historical ecological processes. The authors reported that also the

historical Scandinavian population consisted of these three subpopulations and concluded that the current subdivision is not caused by anthropogenic fragmentation and a genetic bottleneck due to over-hunting. Based on the findings of different studies it is likely the combined effect of ecological processes such as e.g. the density of bears and level of relatedness among individuals in and between areas which can influence the dispersal and successful reproduction of bears outside their natal area. This has been indicated by results assessing kin-related structure (STØEN et al. 2005; 2006; FRANK et al. 2021) and gene flow among the areas in Sweden and Norway (SCHREGEL et al. 2017; 2018). The current anthropogenic pressure, however, may sustain and manifest the current fragmentation further, as it has also been observed in other hunted wildlife species (JERINA/ADAMIC 2008; KROFEL et al. 2012; FRANK et al. 2021). Overall, these results warrant further studies into the history and biology of the Scandinavian brown bear population.

The disconnect of the Scandinavian and Karelian brown bear populations had strong effects on the genetics of both populations (SCHREGEL et al. 2012; KOPATZ et al. 2014; 2021). The genetic differences between these populations become obvious when bears from both populations are genotyped and compared with so-called Y-chromosomal markers (BIDON et al. 2014; SCHREGEL et al. 2015; HIRATA et al. 2017). Analogous to the mtDNA, the non-recombining fragment of the Y-chromosome enables the assessment of the paternal diversity and male lineages. This is of high interest, because such analyses can reveal dispersal patterns as males generally are the dispersing sex in brown bears, while females remain philopatric and tend to stay near their natal area (STØEN et al. 2005; ZEDROSSER et al. 2007). Two recent studies analysed brown bears from the Scandinavian and the Karelian populations and documented strong genetic differentiation between these bear subpopulations as well as that the Y-haplotype diversity was distributed unevenly (SCHREGEL et al. 2015; KOPATZ et al. 2021). As reported by SCHREGEL et al. (2015), Y-haplotype data of bears from Finland, northern Norway and northwestern Russia were high, with 32 haplotypes identified. In contrast, only four haplotypes could be found in the Scandinavian population in Sweden and in western and southern Norway. The haplotype distribution underlined the substantial subdivision of the bear populations in Scandinavia and Karelia (SCHREGEL et al. 2012; 2017; KOPATZ et al. 2014; 2021). Overall, these results suggested that the genetic recovery processes of these two populations have likely been very different (KOPATZ et al. 2021). It is assumed that the Scandinavian bear population recovered to a large extent on its own, while in comparison the Karelian brown bear population in Finland and northern Norway experienced influx from the east, i.e. Russia (TAMMELEHT et al. 2010; KEIS et al. 2013; KOPATZ et al. 2014), which resulted in a population divided into two subpopulations, a northern and a southern one (SAARMA/KOJOLA 2007; TAMMELEHT et al. 2010; KOPATZ et al. 2014). The southern subpopulation showed a strong connection to bear populations in northwestern Russia, supporting the assumption of substantial migration and gene flow from Russia into Finland during the last decades (KEIS et al. 2013; KOPATZ et al. 2014). These high immigration rates, in contrast to the situation in Scandinavia, likely led also to the gradual mixing of these two subpopulations, so that more and more brown bears were showing the genetic signatures from both populations (HAGEN et al. 2015; KOPATZ et al. 2017).

In general, brown bear populations in Scandinavia and in Finland have recovered from population lows at the end of the 19th century (CHAPRON et al. 2014). Based on latest research, the population expansion front with bears from Scandinavia has entered Finland, i.e. bears from Scandinavia have dispersed into Finland (KOPATZ et al. 2021). Also a few individuals from the Karelian population have been detected in Sweden, albeit considerably fewer, suggesting asymmetric migration (Fig. 2). This suggests that the Scandinavian bear population seems to have recovered earlier and therefore started expanding earlier compared to the Karelian population. These results highlight that conservation-oriented policies and wildlife management can lead to successful population recovery as well as the restoration of genetic connectivity between fragmented populations of brown bears (KOPATZ et al. 2021).

Genetic information enabled a large body of scientific literature on the brown bears of northern Europe and has considerably increased the scientific understanding of population genetics as well as underscored the importance of genetics for conservation. Many of the studies presented would not have been possible without the strong collaborative spirit of national authorities and research groups. Especially Norway and Sweden have harmonised the monitoring and their methods and are now equipped with a unique common population monitoring system and database. The brown bear is one of the best-studied mammals in the world (BROOKE et al. 2014), and the Scandinavian brown bear in particular has been of crucial importance in the development of the genetic monitoring of wildlife in general.

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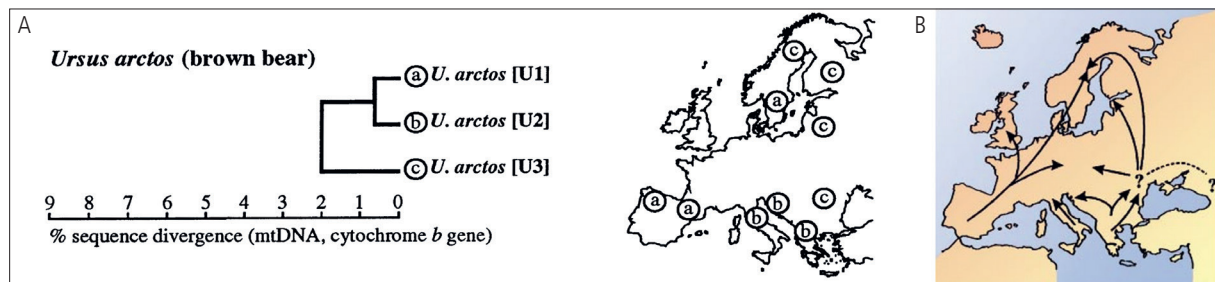


Fig. 1. a: Illustration of the phylogeography of the brown bear across Europe, based on the results by TABERLET/BOUVET 1994 (figure after TABERLET et al. 1998, fig. 2, copyright by Wiley); b: Brown bear postglacial colonisation routes with main refugial areas in Iberia, Italy, the Balkans and the Caucasus (figure after HEWITT 2000, fig. 2, copyright by Nature).

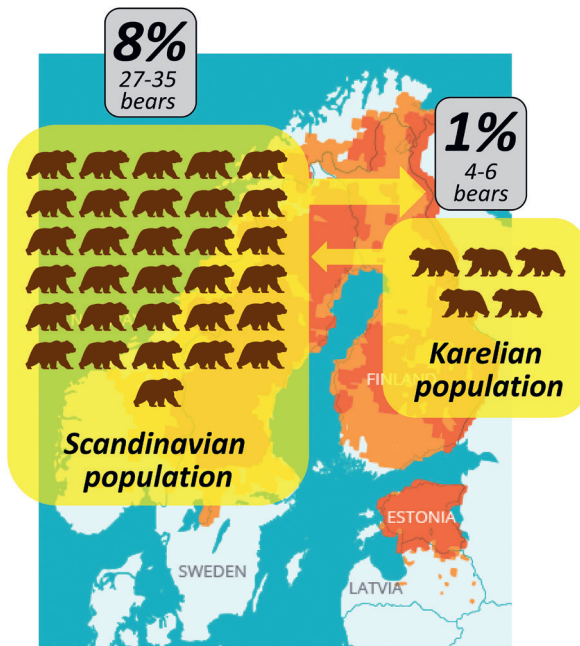


Fig. 2. Illustration of the asymmetric number of migrants per generation between the brown bear populations of Scandinavia (west) and Karelia (east), based on KOPATZ et al. 2021 (background map source: Horizon [modified], distribution data source: Large Carnivore Initiative for Europe, 2012–2016; bear icon by Freepik available on flaticon.com).