

# Prehistoric human impact on wild mammalian populations in Scandinavia

Hans Ahlgren





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Academic dissertation for the Degree of Doctor of Philosophy in Scientific Archaeology at Stockholm University to be publicly defended on Friday 15 October 2021 at 10.00 in Nordenskiöldsalen, Geovetenskapens hus, Svante Arrhenius väg 12 and online via Zoom, public link is available at the department website.

## Abstract

This thesis aims to study the interactions of pre-agricultural societies in Scandinavia with wild mammals, for example in terms of hunting and translocation. More specifically, the aim is to investigate the possibility of identifying examples of overexploitation, targeted hunting or translocation of wild mammals in prehistoric Scandinavia, and to discuss the implications this could have had for both the wild animals and the humans. The thesis also studies translocation to evaluate the feasibility of using it as a proxy for prehistoric human mobility, and to understand the motivation for this action.

Although the focus is on the animals in this thesis, the ultimate purpose is to study humans and their interactions with animals in prehistory. The thesis applies genetic analyses to zooarchaeological material of various mammalian species from different Scandinavian sites, in order to study whether the genetic structures have changed in these species over time, and to assess whether these changes were induced by different human actions. The species studied in this thesis were selected on the basis of the importance they are considered to have had for prehistoric people.

The dissertation comprises five studies. The first study investigates the occurrence of mountain hares on the island of Gotland, and discusses how they got there and where they came from. The second study explores the temporal genetic structure of the grey seal in the Baltic Sea, and discusses whether humans and/or climate were the drivers for the sudden disappearance of grey seals from the island of Stora Karlsö. The third study concerns a shift where moose apparently became less important as prey in northern Sweden at the end of the Neolithic period, and discusses whether humans targeted female moose in hunting. The fourth study analyses and discusses the history of the harp seal in the Baltic Sea. The fifth study is a methodological paper which involves identifying seals according to sex, using the dog genome.

The overall result of the different case studies shows that there were major population fluctuations over time in all the species studied, and that in some cases, humans are likely to have contributed to this, e.g. through overhunting and translocation. The study also shows that the population fluctuations often occurred in connection with certain climatic events, though it was not possible to separate climatic effects from human impact in terms of the cause.

**Keywords:** *hunter-gatherers, Baltic Sea, Mesolithic period, grey seal, harp seal, mountain hare, moose, ancient DNA, hunting, translocation.*

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POPULATIONS IN SCANDINAVIA

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Cover: Mountain hare on Stora Karlsö with the islands of Lilla Karlsö and Gotland in the background. Photo by the author.

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During my time as a PhD-candidate, the ancient DNA field went through a minor revolution. While I started off by studying short DNA-fragments, the discipline evolved towards full genome sequencing in rapid pace. This rendered some of the learnings from my initial time somewhat outdated, which was a bit frustrating, but this methodological evolution also opened up new and previously unthinkable possibilities, greatly improving the quality of the case studies.

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# List of Papers

- I. **Ahlgren, H.**, Norén, K., Angerbjörn, A., Lidén, K., 2016. Multiple pre-historic introductions of the mountain hare (*Lepus timidus*) on a remote island, as revealed by ancient DNA. *Journal of Biogeography* 43: 1786–1796.
- II. **Ahlgren, H.**, Bro-Jørgensen, M.H., Glykou, A., Schmölcke, U., Angerbjörn, A., Olsen, M.T., Lidén, K., (accepted manuscript). The Baltic grey seal – a 9,000-year history of presence and absence. *The Holocene*
- III. **Ahlgren, H.**, Bro-Jørgensen, M.H., Larsson, T.B., Storå, J., Angerbjörn, A., Lidén K, (manuscript). The decline of a Stone Age moose population in northern Sweden
- IV. Bro-Jørgensen, M.H., **Ahlgren, H.**, Puerta, E.J.R., Löugas, L., Gotfredsen, A.B., Glykou, A., Olsen, M.T., Lidén, K. (manuscript). Genomic insights on the Baltic harp seal population.
- V. Bro-Jørgensen, M.H., Keighley, X., **Ahlgren, H.**, Scharff-Olsen, C.H., Rosing-Asvid, A., Dietz, R., Ferguson, S.H., Gotfredsen, A.B., Jordan, P., Glykou, A., Lidén, K., Olsen, M.T., 2021. Genomic sex identification of ancient pinnipeds using the dog genome. *Journal of Archaeological Science* 127, 105321.

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# 1. Introduction

## 1.1 Human impact on the natural environment

Human impact on the natural environment has been particularly extensive in the centuries since industrialisation and its subsequent population growth. It has involved e.g. deforestation, salinisation, acidification, desertification, the depletion of ground water, alterations in land, biological invasions, the depletion of fish stocks, the extinction of species, alterations in the earth system and pollution of the air, land and oceans (Foley et al. 2005; Moran 2006:16pp; Goudie 2013:21). The extent of release of CO<sub>2</sub> in the atmosphere, for example, has been so significant since the end of the 18<sup>th</sup> century that it has been suggested that we have left the Holocene and entered a new geological epoch named the Anthropocene, where humankind is the main global driver of the earth system (Crutzen 2002).

As human impact on the environment has increased during the last centuries, so has interest in the issue of human-related change to the earth, which has become one of the most important themes of our time. It is worth mentioning some early contributors to the discussion on human-related change to the earth. First, George Perkins Marsh's book *Man and Nature* (1864) was a forerunner to the environmental movement. It describes humans as active agents who alter the environment with such thoughtlessness that it threatens their own subsistence. *Man and Nature* was one of the first important accounts to recognise human changes to the environment. A century later, an international conference organised by the Wenner-Gren Foundation for Anthropological Research picked up where Perkins March had left off, aiming to understand the human role in altering the environment. This interdisciplinary conference gave rise to the anthology *Man's role in changing the face of the earth* (Thomas 1956). Its 53 contributors from a variety of fields treat topics which are as current now as they were when the book was written, e.g. land modifications, waste disposal and biological invasions. Interest in the field has grown rapidly during the last decades, but under different flags. There are now several branches of similar, but not identical approaches to studying human interactions with the environment, such as human ecodynamics, historical ecology and cultural niche construction (Laland & O'Brien 2011; Crumley et al. 2017; Fitzhugh 2019). Environmental archaeology emerged as a field in the 1970s, with important contributors such as Karl W. Butzer (1971, 1982),

who highlighted the importance of studying interactions between humans and their natural environment in prehistory.

What, then, has been the result of the last 150 years of concern about human impact on the environment? The vast number of publications and the media attention the topic is receiving show that awareness of the problem is increasing. It is therefore rather ironic that both the rate and scale of human environmental impact have also increased during this period.

This thesis aims to go further back in time in order to shed light on the relationship between humans and their environment. Although prehistoric societies had neither the tools nor the population numbers to be the force of nature that we are today (Steffen et al. 2007), palaeoecological, archaeological and historical records have shown that people in prehistory also affected their natural environment (see e.g. Redman (1999; 2004); Grayson (2001); Diamond (2005) and Kirch (2005)). At a time when the natural environment is exploited in an unsustainable way, it is important to look back and learn from earlier human-environment interactions through the long-term perspective that archaeology can offer. By recognising the consequences that arose from prehistoric alterations of the natural environment, it is possible to identify the difficulties and opportunities which lay ahead of us in our current environmental situation (Tainter 2000:331pp; Boivin et al. 2016).

## 1.2 The potential of interdisciplinary research

The research questions in this thesis could only be answered through contributions from a variety of different disciplines, in this case archaeology, ecology, geology, genetics and climatology. The field of archaeological science, where archaeological hypotheses are studied using scientific methodology, has a long history in the archaeological field (Lidén 2006; Lidén & Eriksson 2013).

A discipline is basically an entity using a shared framework of concepts and methods, where the researchers involved have an interest in similar questions (Aram 2004; Strathern 2007). This framework has the advantage of making a research field easier to grasp, and it also facilitates the evaluation of research within the field (Klein 1990; Bruce et al. 2004). Working across disciplines can remove the limitations of the framework, and hopefully lead to new progress.

Interdisciplinary research distinguishes itself from multidisciplinary research in the sense that, in the former, different disciplines work closely together in an attempt to resolve a common research question which is of interest to each of the disciplines involved. Multidisciplinary research, in contrast, may involve a common research topic, but approaches it from within the frameworks of each separate discipline. This can, but does not necessarily im-

ply cooperation between the disciplines (Bruce et al. 2004). Although interdisciplinary research is challenging, it is an effective method of addressing complex research questions about the past.

### 1.3 Aims and structure of the thesis

The overarching aim of this thesis is to investigate the impact people had on wild mammals in prehistory. However, human impact on the natural environment, such as the destruction or modification of habitats used by wild animals, is also addressed. This aim was honed down to the following research questions:

- *Is it possible to identify the extinction of wild mammalian populations using ancient DNA analyses (aDNA), and to distinguish between overexploitation and climatological factors as the cause?*
- *Is it possible to detect human-mediated transportation of wild mammals in prehistory, and to distinguish this from natural dispersal?*
- *Is it possible to identify targeted hunting of wild mammalian populations in Scandinavia during the Stone Age using aDNA?*

Genetic analyses were performed on ancient skeletal remains of various animal species in order to address the research questions and the issue of human-induced actions. The species studied in this thesis are mountain hare (*Lepus timidus*), grey seal (*Halichoerus grypus*), moose (*Alces alces*) and harp seal (*Phoca groenlandica*), and they were selected on the basis of the economic and/or symbolic importance they are considered to have had for people in prehistory. Their level of importance was defined on the basis of the abundance of each species in refuse material at prehistoric sites, their occurrence in rock art, their depiction on tools, their presence in human burials and their occurrence in places they would not have been able to reach without human-induced transportation. Use of these criteria should only be seen as a way for the author to delimit the thesis. A species may have been important despite not fulfilling the criteria, and other species not studied in the thesis may fulfil one or several of these criteria.

Chronologically, this thesis focuses on the hunter-gatherer societies which dwelt in Fennoscandia during the Mesolithic and Neolithic periods, but examples of human environmental impact from other time periods and geographic locations is also included.

The following chapter will describe and exemplify an array of actions and situations where humans and climatic events affect animal species and their habitat. Chapter three will give an overview of the main archaeological periods studied in the thesis. Although the emphasis of the thesis is on Scandinavia during the Mesolithic and Neolithic periods, the reader will notice that time periods other than these are included, so that there are fewer restrictions in terms of time and space, in favour of a more global perspective. Chapter four explains the methods used in the thesis, with a focus on aDNA analysis. This chapter also provides background information on the archaeological contexts from which the samples were taken. Chapter five introduces the different animal species discussed in the thesis, and presents the results from the case studies. Chapter six summarises the previous chapters, and discusses the case studies in relation to the research questions. Chapter seven is a Swedish summary of the overall thesis.

## 2. Impact on the natural environment

Human impact on wild-animal populations can be categorised as either direct or indirect (Redman 1999:56pp). Direct impact is when human actions directly target the animals, as is the case in domestication, hunting or translocation. Indirect impact is when wild-animal species are affected in different ways as a consequence of human activities, even though this might not have been the purpose. Indirect impact can involve different kinds of land modification which alter the habitats of animals, for example. These categories should be seen as generalisations which have been simplified to obtain an overview of the impact humans have on wild animals. In reality, these divisions are intertwined, so that one kind of impact can have cascade effects in terms of unforeseen events on the ecosystem (Townsend et al. 2008:20).

In discussing the impact humans had on animal species, the negative effects are often emphasised, i.e. negative aspects of habitat disruption or hunting undertaken at an unsustainable rate. Although the negative effects are sometimes obvious, some species may also benefit from human interference. Overexploitation of one species can open up a niche for another, and domestication can increase the size of some animal populations more than would otherwise be possible. Translocation of species to areas with few predators can also be favourable for the translocated species, even if this species has negative effects on the local flora and fauna in its new habitat. It also depends on what counts as beneficial, whether it is quality of life, the spread of genes or other factors (Russell 2011:215p; Goudie 2013:114).

### 2.1 Direct impact

#### 2.1.1 Hunting

Killing an animal probably has the most substantial impact at an individual level. The zooarchaeological material left behind from hunting helps archaeologists visualise this interaction in order to study it. Prehistoric hunting was mainly undertaken for the products that could be extracted from the game, such as skin, meat, bones, antlers, fat, bone marrow and tendons, but there was also a social aspect to hunting, where the hunt itself was as important as the products it yielded (Russell 2011:155pp).

Where a larger proportion of a population is killed or dies from natural causes than the proportion which immigrates or is recruited, it can cause extirpation (local extinction), and even total extinction (Begon et al. 2014:378p). However, for this to take place the hunting pressure must be sustained as the species becomes rare, and there can be no refugia where the species can persist (Owen-Smith 1999:60).

Whether humans caused the extinction of animals in prehistory is a highly debated topic. The most intense discussion has focused on extinction of the so-called mega fauna in the Pleistocene, following the last glacial period. The background to the discussion is as follows. Numerous cases of extinction or extirpation of large, >44 kg, slow-breeding, land-based vertebrates occurred during the last glacial period, c. 50,000-10,000 years ago (Martin 1990; Barnosky et al. 2004; Koch & Barnosky 2006; Grayson 2007; Boivin et al. 2016). While this was a global trend, it was more frequent in some areas than others (Barnosky et al. 2004; Koch & Barnosky 2006). The species which disappeared include the giant wombat (*Diprotodon optatum*) in Australia, the woolly mammoth (*Mammuthus primigenius*) and rhinoceros in Eurasia, and the ground sloth and glyptodonts in the Americas (Koch & Barnosky 2006). There were fewer extinctions in Africa than other continents during the late Pleistocene (50,000-10000 years ago) (Barnosky et al. 2004). The fact that Africa was less affected by extinctions has been interpreted as a result of co-evolution between humans and their prey (Barnosky et al. 2004). A number of theories attempt to explain the disappearance of these animals. One is that human activities such as hunting and landscape modification led to their extinction (Martin 1973; Johnson et al. 2013; Sandom et al. 2014; Andermann et al. 2020). Others emphasise climate oscillations as the probable cause of extinction (Goudie 2013:142pp). Further theories combine human activities and climate change to explain extinction (Barnosky et al. 2004; Koch & Barnosky 2006). The two assumed causes, human impact or climate change, both have their strengths and weaknesses, and the huge time span and geographical area covered make it hard to build a common explanation for extinction. The lack of kill sites (Redman 1999; Grayson & Meltzer 2015), along with the lack of consensus on what constitutes proof of hunting, makes it even harder (Barnosky et al. 2004). The timing of the extinctions varies for different areas, but a connection to human migration can be shown in most areas (Barnosky et al. 2004; Koch & Barnosky 2006). The explanation is that animals in areas that were newly colonised by humans were not accustomed to human hunters, and therefore succumbed easily to predation (Russell 2011:197p; Goudie 2013:142pp).

Doubts about the capacity of human hunters to bring about the extinction of animals at continental level, and the overlap between extinction and global environmental change, have led to a theory which points to climate change, not humans, as the cause of the Pleistocene extinction (Koch & Barnosky 2006). The idea suggests that climate change caused habitat loss, and that this



climate change was too rapid for animals to be able to adapt to the new conditions. However, the theory that climate was the cause has some weaknesses. Firstly, it suffers from the fact that this is not the first shift between a glacial period and an interstadial. Equally, the climate in the Pleistocene did not differ sharply from earlier glacial shifts, but the effect on animal populations was more pronounced (Barnosky et al. 2004; Koch & Barnosky 2006). There are also some doubts about the fact that animals were not able to move to more suitable habitats when the climate change occurred (Goudie 2013:146). Some taxa also survived longer in isolated refugia with a low human presence (Koch & Barnosky 2006). In recent years, the combined forces of climate and human activity have been proposed as the cause of the Pleistocene extinctions (Owen-Smith 1999:67; Barnosky et al. 2004; Koch & Barnosky 2006; Lorenzen et al. 2011; Braje et al. 2017).

The case for the fact that humans caused extinctions is stronger on islands than on continents (Koch & Barnosky 2006). The connection between animal extinctions and the arrival of humans on islands has been demonstrated by several researchers, e.g. Kirch (1982), Steadman (1995), Grayson (2001), Barnosky et al. (2004) and Keighley (2019). Island populations are more vulnerable than populations on the mainland, because they are smaller and are sensitive to the introduction of new species (Grayson 2001). In cases where the extinction of animals has been associated with human colonisation of islands, hunting is probably not the only cause. Manipulation of the landscape and translocation of new species have also been important drivers for extinction (Steadman 1995; Grayson 2001, 2008; Duncan et al. 2002; Koch & Barnosky 2006; Braje et al. 2017).

Conservation practices are intentional strategies constructed to allow a resource to be used without the risk of overexploitation (Smith & Wishnie 2000). A common perception among the general public that indigenous people lived in harmony with nature, using a conservationist approach to their environment to improve the sustainability of the harvest, also exists among certain scholars, e.g. Alcorn (1993) and Hunter-Anderson (1998). Examples of practices include selectively killing individuals that were of less reproductive value, or avoiding overexploitation to preserve biodiversity. There are also examples of long-term sustainable hunting from archaeological sources (Butler & Campbell 2004; Etnier 2007). Calvin Martin (1978:38, 176) describes Native Americans as taking a conservation approach not in terms of avoiding overkill, but out of respect for the spirit of the animals and for fear of retribution. This conservationist approach was eventually abandoned when they began to trade with Europeans (Martin 1978:65).

A true conservation strategy should be distinguished from epiphenomenal conservation. The latter has the same effect as a conservation strategy, but is driven by different motives. Epiphenomenal conservation is not a conservation strategy but a side effect of circumstances which limit resource use, e.g.

the migration patterns of the hunters, or the result of demographic or technological factors (Alvard 1993; Hunn 1999:165pp). Ethnological studies of present-day subsistence hunters show a variety of strategies for selecting prey in different hunting communities. Valley Bisa hunters in Zambia consciously selected male animals because the yield was higher (Marks 1973). Studies on the Piro in the Peruvian Amazon showed that hunting focused on the abundance of animals rather than sex (Alvard 1995). Among the Machiguenga in the Peruvian Amazonas, there was no taboo on killing either female animals or animals that were pregnant (Smith 2001). Subsistence hunters in the Brazilian Amazon preferred to hunt pregnant females because their infants could be sold as pets (Peres 1990). Converting the results from ethnographic studies to a prehistoric setting is highly problematic and not straightforward. It can nevertheless be useful to see how human hunting strategies can vary according to environmental preconditions.

Selective hunting has been identified in archaeological material from different time periods and geographical locations. For example, Kay (1994, 1997) claimed that native populations in North America selectively killed ungulate cows because of the superior quality of the meat and hides. A study of wild boar (*Sus scrofa*) hunting in four Mesolithic sites in Sweden showed that the hunt had concentrated on adult females at two of the sites, and on juveniles of both sexes at the other two sites (Magnell 2005). The aim of the hunt was interpreted as optimising yield rather than sustainability (Magnell 2005). Analyses of the bone material from a Mesolithic site in Friesack in northern Central Europe revealed that the hunt there focused on female roe deer (*Capreolus capreolus*) and wild boar and this was interpreted as being the result of different behaviour in females and males (Schmölcke 2019:1pp). The reproductive value of different sub-categories within a population is different, which means that selective harvesting can have an effect on the long-term survival of a population (Caughley 1977:188pp). Targeting males, for example, has less effect on the survival of the population than if females are selected (Caughley 1977:188pp). This is particularly true for mammalian species which have a polygynous mating system where one male mates with several females (Lyman 2003). Selective harvesting by age, which involves killing juveniles, can also have a harmful effect on the survival of a population, since juvenile survival determines recruitment to future generations (Gailard et al. 1998).

### 2.1.2 Translocation

Wild animals can disperse into new areas either through natural dispersal or human-induced translocation. Dispersals are usually slow and continuous processes which have always occurred, and the gradual nature of the process has facilitated adaptation to the new landscapes. Natural dispersals can be halted by geographical obstacles such as large bodies of water, mountains or deserts,

but with human translocation, animals can cross these barriers (Redman 1999:59pp; Nentwig 2007:11). The International Union for Conservation of Nature (IUCN/SSC 2013) defines translocation as follows:

“Translocation is the human-mediated movement of living organisms from one area, with release in another.”

This definition includes both intentional and unintentional translocation, and both wild and captive organisms.

Humans have a long history of moving organisms to areas beyond their natural habitats, though it is still surprising to see the wide range of vertebrates, invertebrates and plants that were introduced to new areas by humans in prehistory. Although the oldest record of translocation dates back to 19,000 years ago, the custom of translocation became increasingly more common from the Holocene onwards (Grayson 2001). Studying translocation makes it possible to use the organisms as proxy evidence for how humans have moved around in prehistory (Larson 2017). This can be done using molecular methods such as DNA or stable isotopes, e.g. strontium, sulphur or oxygen, preferably supported by radiocarbon dating (Storey et al. 2013). The field of aDNA has led to new opportunities for analysing the history and descent of different taxa. Using aDNA, the modern population of an organism can be compared to its ancient counterparts in the same area, allowing studies of changes in population structure that would not otherwise be possible, such as extinction and recolonisation. To study migrations, aDNA from an organism at an archaeological site is compared to contemporary organisms from other areas. In this way, the ancient movement patterns of the organism can be elucidated. Data from aDNA of both wild and domesticated mammals have been used as proxies to track migration patterns of ancient human populations (Larson 2017).

Questions like how, when and from where different animal taxa arrived in an area have fascinated researchers in different fields for a long time. These questions especially attract attention in areas surrounded by a natural geographical border where there is no obvious answer to how the animals arrived, as is the case with the fauna on Madagascar (Vences 2004; Samonds et al. 2012) or the Falkland Islands (Austin et al. 2013). Apart from human-mediated translocation, the occurrence of animals on remote islands is commonly explained by natural dispersals through rafting on floating debris, swimming, flying or migration over a land bridge which was ultimately submerged (Samonds et al. 2012; Storey et al. 2013). In areas such as Scandinavia, walking on ice could also be a possibility. The biological properties of different species affect the likelihood of natural dispersal. Some species are limited by their metabolic requirements, making a long trip over a sea impossible, while others are too large for rafting (Hofman & Rick 2018). In addition, some species do

not naturally disperse and do not undertake long-distance dispersals. A prerequisite for studying prehistoric translocation is that the organism was not present in the study area prior to human colonisation (Grayson 2001). For this reason, the majority of studies on prehistoric translocation have analysed the fauna on islands. See, for example, studies on islands in Oceania (Heinsohn 2003; Zerega et al. 2004; Larson et al. 2007; Storey et al. 2010; Fillios & Tacon 2016), the Mediterranean Sea, (Valenzuela & Alcover 2013; Vigne et al. 2016; Lalis 2019), the Caribbean (Giovas et al. 2012; Kemp et al. 2020) and islands in the North Atlantic (Searle et al. 2009; Jones et al. 2012). There are also examples from Scandinavia and the island of Gotland in the Baltic Sea (Fraser et al. 2012; **Paper I**). Gotland is particularly well suited for these kinds of study, since it was covered by ice during the last glacial period and later submerged under water. It has had no connection to mainland Sweden, and therefore has no native fauna.

The list of human-mediated instances of translocation of mammals is vast, and will not be fully reviewed here, but two important examples will be mentioned. One animal which has humans to thank for its global dispersal is rats. The prehistoric dispersal of the Pacific rat (*Rattus exulans*) in Oceania has been thoroughly studied by e.g. Barnes et al. (2006), Matisoo-Smith & Robins (2004, 2009), Wilmshurst et al. (2008) and Anderson (2009). This spread of the Pacific rat between the Pacific islands is likely to have been intentional, since the rat seems to have been an important source of protein (Matisoo-Smith & Robins 2004; Commendador et al. 2013). It is believed that the Pacific rat had a huge impact on the native flora and fauna where it was introduced (Steadman 1995; Athens et al. 2002; Gibbs 2009), and has even been accused of contributing to deforestation (Hunt & Lipo 2009). From a human perspective, the impact of the dispersal of the black rat (*Rattus rattus*) was considerable, with its connection to diseases such as the bubonic plague (Yu et al. 2021).

Another group of animals which was translocated extensively involves lagomorphs. These include hares and rabbits, and lagomorphs have probably been the most popular group of animals for translocation by humans, as demonstrated by the hundreds of examples of introduction to new areas (Flux & Fullagar 1992; Kasapidis et al. 2005; Suchentrunk et al. 2006; Masetti & De Marinis 2008; Montgomery et al. 2014; Seixas et al. 2014; Mengoni et al. 2018). Lagomorphs have a long history as a popular game species, and their modest demand for space and high reproduction rate often made translocation successful.

In terms of the translocation of different floral species, it has been suggested that the swift spread of hazelnut (*Corylus avellana*) in northern Europe after the last glaciation was aided by humans (Iversen 1973). The rationale for this is that hazelnuts are often found in refuse materials at Mesolithic sites, and seem to have been an important food resource (Regnell 2012). This idea has been widely debated, since it is also possible that hazel spread naturally,

and because hunter gatherers are highly mobile, where growing a hazel tree takes time (e.g. Tallantire 2002; Bishop et al. 2015; Groß et al. 2019; Apel & Storå 2020).

The reason for introducing a species to a new area certainly differed according to the species, and has also varied through time and place. In broad terms, the aims of moving wild animals in modern times have been to introduce, re-introduce or re-stock a population (Griffith et al. 1989). Looking at these categories more closely will, however, reveal a variety of different motives for modern translocation, such as keeping pets, biological control or the introduction of wild game and domesticated species (Redman 1999:59pp; Long 2003:xii; Nentwig 2007:11; Goudie 2013:115pp; Begon et al. 2014:387pp). The motives for translocation in prehistory are more likely to have involved the fact that the species was used as a food resource, for toolmaking or in rituals, for its fur or as pets (Giovas 2019). It has also been suggested that animals and plants have been introduced to locations colonised by humans, in order to mimic the landscape they came from, a phenomenon known as transported landscapes (Kirch 1982; Redman 1999:59pp; Storey et al. 2013; Hofman & Rick 2018). This is regarded as active manipulation of the landscape with the intention of making the new environment more familiar. Once transported to an island, the wild animal could be released to establish a new population which could later be hunted (Russell 2011:273pp; Vigne et al. 2016). There are also examples where domesticated animals have been set free or escaped, to establish a feral population (Savolainen 2004; Russell 2011:273pp).

The introduction of species can also be unintentional, as flora and fauna can accompany migrating humans in their cargo, and thus spread to new areas without the knowledge of the transporter (Kirch 1982; Redman 1999:59pp; Nentwig 2007:11pp; Goudie 2013:117pp). This has often been the case when organisms seen as pests have been translocated, such as insects or pathogenic organisms (Redman 1999:53pp; Long 2003:xiii; Boivin et al. 2016; Yu et al. 2021). Species which have a deteriorating effect on the landscape they are moved to are considered invasive (Mack et al. 2000), and have exacted a high ecological and economic cost globally in modern times (Pimentel et al. 2005; Begon et al. 2014:387pp). It has also been shown that animal species which have been introduced to new areas can change the behaviour and evolutionary trajectory of native taxa (Sullivan 2017).

### 2.1.3 Domestication

This thesis does not directly address domestication, but the topic deserves to be mentioned for two reasons. Firstly, the domestication of wild-animal species represents one of the most substantial impacts humans have had on mam-

malian species. Secondly, aDNA has significantly contributed to answers involving the domestication of different species, and has solved major archaeological and anthropological issues.

The huge impact that domestication has had on the development of human society, and the huge body of literature which discusses the topic, tend to give the impression that there is general consensus on how the concept of domestication should be defined. Unfortunately, this is not the case. To complicate matters further, the concept of domestication has both a biological and a social dimension (Russell 2011:208). The biological dimension emphasises the process which takes place when an organism is selectively bred to meet the needs of people, based on its phenotypic traits. This often involves elements of time, and control of movement and breeding (Russell 2011:208pp). The social dimension of domestication focuses on relations of ownership of domesticated species in comparison with their wild counterparts. Here, wild organisms are described as shared resources, where domesticated animals have owners who invest time and energy in them (Ingold 1980:4p; Russell 2011:212p; Outram 2014:750p). Diamond (1999:159) gives the following definition of domesticated animals:

“an animal selectively bred in captivity and thereby modified from its wild ancestors, for use by humans who control the animal’s breeding and food supply”.

This is a very general definition, but it covers the most important aspects of domestication in terms of its direct impact on animals. It could be added that it is a multigenerational process which acts on the population level. One of the reasons why it is difficult to define domestication is that there are relations between humans and animals which fall in the middle of the scale from wild to domesticated (Dobney & Larson 2006). There is a gradient between wild and domesticated, and the terms cannot therefore be considered strict opposites (Dobney & Larson 2006). Furthermore, some animals, e.g. the house mouse (*Mus musculus*) or the brown rat (*Rattus norvegicus*), prefer to live within the human sphere, and could thus be considered domestic even if humans have not taken active steps to let them in (Russell 2011:211).

Many species that spend their life within the human sphere are not domesticated but tamed. The distinction between a domesticated and a tamed animal is that the first is born in captivity while the latter is born in the wild (Diamond 1999:159; Russell 2011:209). Taming does not alter the morphological properties of the animal, since this relationship does not prevail over generations, and it does not affect the species on a population level. Examples of species which are often tame but not domesticated include elephants (Elephantidae).

As a matter of fact, not all species can be tamed, and even fewer can be domesticated. It is the characteristics of the species which determine whether it can be domesticated, and several lists of animal characteristics important for

domestication have been outlined over the years. The first was written in the mid-19<sup>th</sup> century (Galton 1865). The following list of characteristics favouring domestication was defined by Diamond (1999), and should be seen as general rather than strict rules.

1. *The diet.* The animal intended for domestication should preferably be a herbivore or omnivore, simply because it is not economically feasible to breed carnivores for their meat.
2. *Growth rate.* Fast growth rate is key for domestication since it is a process that spans generations.
3. *Reproduction in captivity.* Some animal species refuse to mate in captivity because of complex mating rituals.
4. *Temperament.* Animal species with a temper are hard to domesticate, and attempts can be dangerous or fatal for humans.
5. *Tendency to panic.* It is difficult to keep species in captivity if they are easily stressed.
6. *The social structure of the animal.* It is easier to domesticate animals that live in flocks and have a hierarchy where they can accept humans as leaders.

(Diamond 1999:169pp).

The way in which domestication occurred is most likely to have differed between species. It has been suggested that domestication was not deliberate, but rather a consequence of a symbiotic relationship induced by animals which sought human contact, or which utilised the niches humans created (Russell 2011:215pp; Larson & Fuller 2012). Another theory is that the young of different species were kept as pets and eventually bred in captivity (Russell 2011:215pp). There are different reasons for choosing to keep a particular species in captivity. Some species are kept to secure the supply of food or wool, while others are used as an aid to work, or used in feasting or religious practices (Russell 2011:215pp). Once in captivity, the species can be selected on the basis of preferred traits (Larson & Fuller 2012).

It is believed that common species like dogs (*Canis lupus familiaris*), sheep (*Ovis aries*), goats (*Capra hircus*), cattle (*Bos taurus*), pigs (*Sus scrofa domestica*), chickens (*Gallus gallus*), horses (*Equus caballus*) and water buffalo (*Bubalus bubalis*) were the first to be domesticated (Diamond 1999:159pp; Russell 2011:208; Larson & Fuller 2012; Goudie 2013:36; MacHugh et al. 2017). However, a problem with deducing the timing of domestication is that it is difficult to determine when an animal became domesticated based on morphology. Even though domesticated animals often look different morphologically from their wild relatives, this information cannot be used to determine events leading to domestication since this process takes time. One way of identifying domestication is by studying mortuary patterns and defining the

age and sex of the animals (Smith 2007; Russell 2011:256pp). The composition of the zooarchaeological material from domesticated species is biased towards older females, while males are killed off at an earlier age (Zeder 2001; Zeder et al. 2006).

Other questions concerning domestication involve whether a species has been domesticated on one or several occasions, and where the events involving domestication occurred (Savolainen et al. 2002). The centre of domestication is believed to house considerable genetic variation, but this declines further away from the centre. On the other hand, the genetic or genomic data are not always as straightforward as they could be (MacHugh et al. 2017), since gene flow has taken place between wild and domesticated species throughout history (Larson & Fuller 2012; MacHugh et al. 2017). Traces of domestication can also be identified by studying ancient genomes, searching for selection on certain traits which are believed to be connected to domestication (MacHugh et al. 2017), or comparing DNA from prehistoric and modern populations (Brown & Brown 2011:215).

The examples of direct impact described above can be harmful for mammalian populations in some cases, yet the most deleterious consequences for mammalian populations derive from indirect impacts such as alterations in habitat (Caughley 1977:200p).

## 2.2 Indirect impact

### 2.2.1 The transformation of landscapes

Throughout history, alterations in landscape caused by human activity have had a severe impact on the natural environment. Some animals, e.g. beavers (Castoridae), also change their habitats, though human-induced changes to the landscape are by far the greatest (Townsend et al. 2008:424pp). Alterations in the landscape can affect individual species by destroying or reducing their habitat, or by making it more fragmented (Townsend et al. 2008:460pp; Goudie 2013:133pp). To say that human-induced landscape transformations are always disadvantageous would be an oversimplification, as the alterations may, in some cases, prove beneficial to some species. One example of this involves the clam gardens on the east coast of North America, where people introduced a novel approach to increasing food production by modifying the natural habitat for clams. They began to build walled terraces of rock in the sea 3,500 years ago, to optimise the conditions and increase the areas suitable for clams, usually butter clams (*Saxidomus gigantea*) and littlenecks (*Protothaca staminea*) (Smith et al. 2019; Toniello et al. 2019). These landscape modifications increased the number of clams and established a stable food supply for the people who built them (Smith et al. 2019; Toniello et al. 2019).



Fires have always occurred naturally; they can be beneficial and lead to increased productivity and higher levels of species diversity (Goudie 2013:53pp). By ‘taming’ fire, humans developed a powerful tool for modifying the landscape. Extensive prehistoric use of fire has been documented in Australia and New Zealand (McGlone & Wilmshurst 1999; Bliege Bird et al. 2008; Pausas & Keeley 2009; Baillie & Bayne 2019). People have utilised fire for a number of reasons, such as domestic use, hunting, making grassland suitable for wild and domesticated animals, and clearing the land for agriculture (Stahl 1996; Hayashida 2005; Bliege Bird et al. 2008; Boivin et al. 2016; Baillie & Bayne 2019). There are examples where people cleared forests to attract game already during the Mesolithic period in Britain (Hayashida 2005). Fires can alter and reduce habitats for many species, although a burned area can also return to its former appearance if it is left to regenerate (Baillie & Bayne 2019).

The introduction of agriculture was an important event in the development of humankind, with many social implications such as sedentary living, urbanisation and population growth. The onset of agriculture also transformed the habitat of many animal species and greatly altered prehistoric environments, for example by degrading soil, and has even been linked to extinctions (Hayashida 2005; Hansford et al 2021). With agriculture came the need to control the water supply by building terraces on slopes or sophisticated water canals (Stahl 1996).

Easter Island, or Rapa Nui, has been described as an example of the destruction of a prehistoric habitat which eventually led to the collapse of the society there, and is viewed as a cautionary tale for what could happen to modern society. However, it is not easy to determine whether people, climate change or rats (Hayashida 2005; Diamond 2007; Hunt & Lipo 2009; Mieth & Bork 2010) were to blame for the prehistoric societal crisis the island experienced.

## 2.3. The forces of nature

### 2.3.1 Extraordinary events

The previous chapters described situations and events where humans interfered with the life of wild animals. However, humans are not always responsible for altering animals’ living conditions. This can be said for both prehistoric and modern contexts. Events beyond the control of humans, such as natural disasters and climate oscillations, have historically played an important part in changing the environment for animals and plants, as well as for humans. This has sometimes had global implications, as in the case of the asteroid impact during the Cretaceous, some 65 million years ago (Barnosky et al.

2011). Tectonic activity is an important force of nature which can lead to a series of disasters at the tectonic-plate boundaries. Tectonic activity can cause volcanic eruptions with devastating effects in the proximity of the eruption, such as lava, fast-moving gas currents, falling tephra and mudflows, but it can also have effects on a global scale. Examples include the famous eruption of Vesuvius in 79 BC, where falling tephra covered a huge area including the ancient cities of Pompeii and Herculaneum. Less known to the general public is the Laacher See eruption which occurred in western Germany in c. 11,000 BC, and which covered the immediate surroundings with tephra up to 50 metres in depth, stretching hundreds of kilometres from the eruption site (Baales et al. 2002; Riede 2016; Niemeier et al. 2021). It has been proposed that the eruption had dire consequences for contemporary hunter-gatherer populations in northern Europe, as they abandoned large areas (Riede 2008, 2016). Animal tracks have been discovered in the tephra layer, and although it is difficult to estimate the ecological consequences of the Laacher See eruption (Baales et al. 2002), it almost certainly affected the animal species that dwelt in the area. Volcanic eruptions can also affect the environment on a regional and even global scale through reduced solar radiation (Stahl 1996; Goudie 2009:355pp). It has been suggested that the 536 AD cooling event in the northern hemisphere was the result of one or several volcanic eruptions and the reduced solar radiation that followed (Larsen et al. 2008).

Earthquakes are another great force initiated by tectonic activity. They can cause changes in land levels and have a negative effect on ground water. In coastal areas they can also cause a tsunami (Stahl 1996; Goudie 2009:373pp). The best-known prehistoric tsunami event is probably the Storegga tsunami. This was caused by a massive underwater landslide off the coast of Norway c. 6,100 years BC (Bondevik et al. 1997; Dawson et al. 2011). The tsunami that followed hit the Norwegian coast with a wave up to 11 metres in height, but the Faroe and Shetland Islands and the British Isles (including Ireland) were also affected (Dawson et al. 2011).

Another factor that could have had devastating effects on wild-animal populations in prehistory involves epizootic outbreaks. In modern times, there are examples where wild-animal populations have been severely affected by this. Seal populations in northern Europe, for example, suffered outbreaks of the phocine distemper virus in 1988 and 2002, causing the death of tens of thousands of harbour seals (*Phoca vitulina*) (Kennedy 1998; Härkönen et al. 2006). However, it is difficult to assess the role diseases played for wild-animal populations in prehistory, although aDNA analyses could play a role in understanding these kinds of process in the future.

### 2.3.2 The ever-changing climate

Different weather phenomena have a great impact on different organisms. At a local level, these include meteorological forces such as storms, tornadoes, floods or droughts, but climatic oscillations can also affect large geographical areas. The climate has varied continuously since the Last Glacial Maximum (LGM). The later part of the Pleistocene and the Holocene have been divided into different chronozones based on these variations. Based on Mangerud et al. (1974), the division is as follows, converted from radiocarbon years BP (summarized in Fig. 1)

- Bølling, 13,500–12,000 cal BC. The ice cover in southern Sweden retracted and a steppe landscape started to form as different flora entered the new domain. The climate is described as subarctic/temperate.
- Older Dryas, 12,000–11,750 cal BC. This period is characterised by deterioration into an arctic climate.
- Allerød, 11,750–11,000 cal BC. The climate is again characterised as temperate, with deciduous forest in southern Sweden, starting to advance north.
- Younger Dryas, 11,000–9,700 cal BC. A significant deterioration in the climate occurred during the onset of this period, resulting in constant permafrost and receding flora and fauna. At the end of this phase the climate gradually improved again.
- Preboreal, 9,700–8,100 cal BC. The climate during this period was warmer than the current one, and flora and fauna were once again able to colonise Sweden.
- Boreal, 8,100–6,900 cal BC. The continued warm climate during this period caused the last ice sheet in northern Sweden to melt.
- Atlantic, 6,900–3,900 cal BC. This period is described as warm, with temperatures 2–4°C higher than today, with the exception of the 8.2k event which led to a colder climate for a couple of hundred years, marking the beginning of the Middle Holocene. The forests were dense, with heat-demanding trees spreading further north than their current extension.
- Sub-boreal, 3,900–600 cal BC. The 4.2k event led to a colder and wetter climate phase during this period.
- Sub-Atlantic, 600 cal BC–present. The climate fluctuated between cold and warm periods during this phase. A cold period called the Little Ice Age occurred between AD 1450 and AD 1850.

These divisions were based on radiocarbon dates from palaeontological data from sediments, but are nowadays based on the chronology from Greenland ice cores (Björck et al. 1998; Rasmussen et al. 2006). The chronozones are

characterised by shifts between colder and warmer periods, but temporary climatic events of only a few hundred years also occurred during these phases. Two temporary events of this type occurred in the study area during the periods covered by the thesis. The first is the 8.2k event, which was an abrupt cooling event in 6,200 cal BC, likely to have been caused by a release of meltwater into the North Atlantic which affected the North Atlantic current (Alley et al. 1997; Alley & Ágústsdóttir 2005). The cooling event is believed to have lasted for 200 years, and had a severe impact on the environment (Anderson et al. 2013:172p). Not only did this event have a negative impact on the climate, it also caused a global rise in seawater, with devastating effects on societies living close to the ocean (Anderson et al. 2013:173). The second significant climatic event with a global impact occurred in 2,200 cal BC, and is known as the 4.2k event (Walker et al. 2012). This event manifested itself differently in different parts of the world (Walker et al. 2012). In northern and Central Europe, it caused a fluctuating climate with lower summer temperatures and increased precipitation (Hammarlund et al. 2003; Jessen et al. 2005; Andersson et al. 2010; Walker et al. 2012). The reason for the 4.2k event is not as clear as for the 8.2k event (Walker et al. 2012). The 8.2k and 4.2k events had such a significant global impact on the climate that these events are used as subdivisions of the Holocene into Early (starting at 11.7k), Middle and Late Holocene (Walker et al. 2012, 2019; Fig. 1).

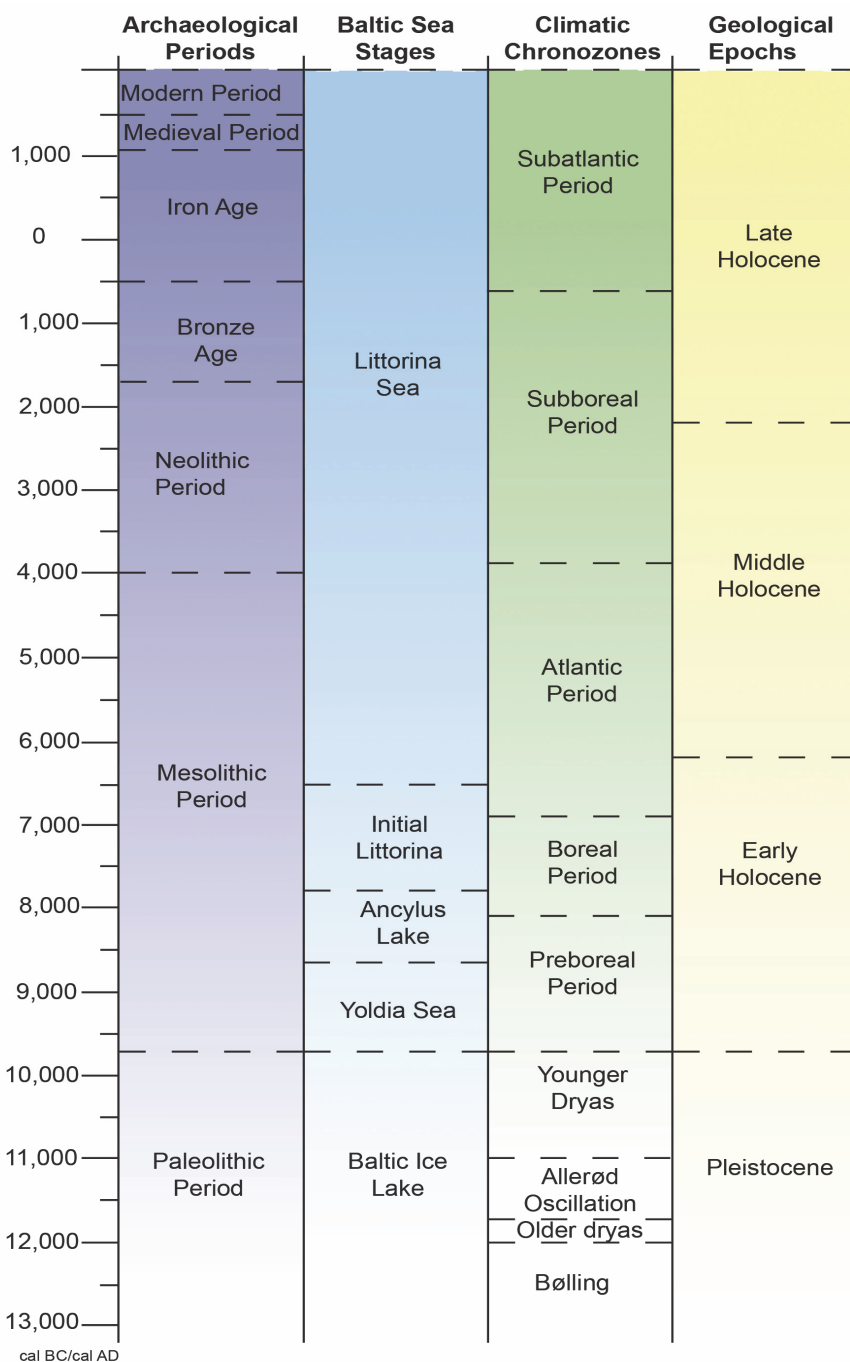


Figure 1. The connection between Archaeological periods, Baltic Sea stages, Climatic Chronozones, and Geological Epochs in Fennoscandia stated in cal BC/cal AD. Based on data from Mangerud et al. 1974; Berglund et al. 2005; Walker et al. 2012; Nationalencyklopedin, accessed 2021-09-12.

### 2.3.3 The history of the Baltic Sea

Most parts of the Fennoscandian Peninsula were covered by ice during the last glacial period, which lasted from 110,000 to 9,300 BP (Andersen & Schack Pedersen 1998; Aaris-Sørensen 2009). At its maximum, some 20,000 years ago, the ice rim stretched down to 52° N with a zone of permafrost south of this rim. A series of different stages followed the end of the glacial period in the Baltic basin, driven by deglaciation, isostatic rebound, variations in global sea level and climatic changes.

In the first stage (Fig. 1), the Baltic basin was filled with water from melting ice, creating a large freshwater lake known as the Baltic Ice Lake (~14,000–9,700 cal BC). Few microfossils have been found from this stage, which implies that the Baltic Ice Lake did not support much life. The Baltic Ice Lake had an outlet through Öresund, but the isostatic rebound in the south lifted the Baltic Ice Lake above the global sea level and eventually closed the outlet (Björck 1995; Andrén et al. 2011). Drainage was created in central Sweden around 11,000 cal BC in areas which had previously been suppressed by the ice sheet, so that water from the Baltic Ice Lake could reach the sea in the west. This situation was only temporary, as the ice sheet started to advance and eventually closed this outlet during the cold phase of the Younger Dryas. A second period of drainage of the Baltic Ice Lake occurred around 9,700 cal BC, and this marks the beginning of the next phase in the Baltic basin, the Yoldia Sea (~9,700–8,700 cal BC) (Andrén et al. 2011:84). The initial outflow of water lowered the sea level of the Baltic basin by 25 metres (Björck et al. 1996; Hansson et al. 2018), and a land bridge was created connecting Sweden to the continent, making it possible for non-volant mammals to enter Sweden. Tree stumps and archaeological finds can be found today below sea level in the southern Baltic Sea, showing that the sea level was lower than today (Rosentau et al. 2017; Hansson et al. 2018). The Yoldia Sea was on a level with the global sea level, and at times more saline water entered in central Sweden, as seen in finds of the marine-living mollusc *Yoldia arctica* in sediments from this period, which gave the period its name (Björck 1995; Andrén et al. 2011:84).

The phase that followed was also named after a mollusc: the term Ancylus Lake (~8,700–7,800 cal BC) comes from the freshwater mollusc *Ancylus fluviatilis*, which is found in the sediments from this period, indicating that the Baltic basin had once again become a lake (Björck 1995; Berglund 2005; Andrén et al. 2011:84p). Isostatic uplift disconnected the inflow of saline water in central Sweden, and dammed the Ancylus Lake so that the sea level became higher than the global sea level (Andrén et al. 2011:87). The uplift in the north caused the Ancylus Lake to tilt, inducing a transgression phase in the south. The masses of water eventually found their way through the Danish isles, creating a new outlet called Dana River. This also resulted in the disappearance

of the land bridge that connected Sweden to the continent (Björck 1995). Following the Ancylus Lake was a phase of low inflow of saline water called the Initial Littorina Sea ~7,800–6,500 cal BC (Andrén et al. 2000, 2011:88; Berglund et al. 2005). During this period, the ice sheet that had covered Scandinavia finally melted, and the organic content in the Initial Littorina increased. The timing of the shift between the Ancylus Lake and Littorina Sea is uncertain and debated (Andrén et al. 2000, 2011; Berglund et al. 2005; Bennike et al. 2021). The next stage is known as the Littorina Sea, named after the sea snail *Littorina littorea*, and is most likely to have been caused by a eustatic rise in sea level, in turn caused by melting ice sheets which pushed saline water into the Littorina Sea, creating a brackish sea with a higher organic content than the previous period (Björck 1995; Berglund et al. 2005; Andrén et al. 2011:88p). The Littorina Sea experienced several transgression and regression phases, but the sea level was generally higher than it is today (Berglund et al. 2005). The salinity of the Littorina Sea gradually increased until it reached its highest level ~4,800–4,200 cal BC (Berglund et al. 2005). This complicated natural history is also reflected in the fauna and flora present in this area during the different phases.

### 3. Scandinavia during the Stone Age

This study covers the period from the first phase of human settlement of the Scandinavian Peninsula during the beginning of the Mesolithic period, through the Neolithic period to the end of the Stone Age. The following section involves a brief overview of the general patterns seen in the study area after the end of the glacial period.

#### 3.1 Human and animal settlement in Sweden

As the ice retreated after the LGM, flora and fauna could advance from the refugia where they been living during the glacial period. These refugia were located on the Iberian Peninsula, in Italy, in the Balkans and in a region in the Caucasus (Hewitt 2004). Among the first mammalian species to reach southern Sweden were those which were adapted to the cold, such as the woolly mammoth, reindeer (*Rangifer tarandus*), mountain hare and arctic fox (*Vulpes lagopus*) (Hewitt 2004). Fennoscandia was colonised from both the south and the north, but the travel route varied for different species (Ekman 1922:435p; Jaarola et al. 1999; Hewitt 2000). Reindeer bones have been found at a number of early sites in Fennoscandia, and the importance of this species for the settlement of both north and south Scandinavia has been stressed (Larsson 1990; Bergman et al. 2004; Aaris-Sørensen et al. 2007; Hedman 2009; Möller et al. 2012; Wygal & Heidenreich 2014; Ekholm 2021).

As was the case for animal species, the first hunter-gatherer populations entered the Scandinavian Peninsula from several directions, from the south of Sweden via the coast of Norway (Zvelebil 2008; Möller et al. 2012; Wygal & Heidenreich 2014) and possibly via an eastern route from northern Finland and the Kola Peninsula (Bergman et al. 2004; Rankama & Kankaanpää 2008; Riede 2014). The colonisation of the new land by both animals and humans is likely to have occurred in pulses, with alternating expansions and contractions rather than a continuous expansion (Aaris-Sørensen 2009; Riede 2014). The ice sheet remained the longest in the interior of northern Sweden (Bergman et al. 2004), so this area was inhabited somewhat later than the rest of Fennoscandia. Analyses of aDNA have shown that the genetics in early hunter-gatherer groups in Scandinavia were a mix of haplogroups from western and eastern Europe (Günther et al. 2018).



## 3.2 Northern Sweden

The oldest sites in northern Sweden date to c. 8,000–7,500 cal BC, and are described as field camps lacking in visible construction features (Bergman 2004). The subsistence of these early people seems to have concentrated on reindeer (Bergman 2004; Ekholm 2021). During the late Mesolithic and Neolithic periods, a characteristic dwelling structure appeared which became common in northern Sweden: semi-subterranean structures with surrounding embankments (Lundberg 1997:118pp). These are made up of a dugout area encircled by a wall of soil, fire-cracked stone and other waste products that have been discarded and placed around the pit, probably to improve the cover (Lundberg 1986:81pp; Spång 1997:87pp). This type of building is not limited to northern Sweden, but has an almost circumpolar distribution with a strong link to the boreal forest belt (Mökkönen 2011:20pp). In northern Sweden, these structures are linked to moose hunting, since the majority of bones found at these sites derive from moose, followed by remains of beaver and reindeer (Lundberg 1997:123pp). This stands in sharp contrast to contemporary coastal sites in northern Sweden, where bones from ringed seal (*Phoca hispida*) are more abundant (Ekman & Iregren 1983:38p; Baudou 1992:64p). The connection between moose hunting and the semi-subterranean structures is also shown by the elaborate systems of hunting pits which are often found in proximity to the embanked sites (Rydström 1984; Spång 1997:73pp; Lundberg 1997:123pp). Although there are problems fitting the hunting pits into a certain time period, they have been shown to be located near contemporary migration routes for moose (Spång 1997:60pp).

The end of the Neolithic period, involving the centuries around 2,000 BC, seems to have been a period of considerable societal change in the interior of northern Sweden (Baudou 1977:144p). The large, semi-subterranean houses disappeared, and the dwelling houses became smaller and were located in other places in the landscape (Forsberg 1985:276pp; Forsberg 1988; Baudou 1992:95pp; Lundberg 1997:118pp; Larsson et al. 2012). During this period, ceramics made their appearance in the area, and tools of an eastern origin became common (Baudou 1977:144p; Baudou 1992:95pp; Nyqvist 2007; Larsson et al. 2012). Based on the composition of the refuge waste dumps around the dwelling houses, it seems that the moose had lost its position as the main prey, and skeletal remains from other wild animals are predominant (Forsberg 1985:275pp; Forsberg 1988; Storå et al. 2011:57; Larsson et al. 2012). The depiction of moose on tools and rock art also comes to an end during the period (Baudou 1992:88pp; Larsson et al. 2010a). Equally, moose seem to disappear from the zooarchaeological material in both Norway (Rosvold et al. 2009) and Finland (Ukkonen 1993) c. 2,000 cal BC.

### 3.3 Southern Sweden

The Stone Age in southern Scandinavia is different from its northern counterpart, as food was mainly procured through hunting and fishing throughout the Stone Age in the north.

The discussions concerning the Mesolithic Period in southern Sweden are often dealing with the different cultural complexes present during this period, distinguished from each other by their material culture. These cultural complexes include the Maglemose culture during the Early Mesolithic, the Kongemose during the middle Mesolithic and Ertebølle culture during the Late Mesolithic (Rowley-Conwy 1999; Zvelebil 2008). In terms of the island of Gotland, the earliest evidence of human presence derives from the cave of Stora Förvar, situated on the island Stora Karlsö, located a few kilometres off the west coast of Gotland (see chapter 4.3.1). The stone artefacts that have been found in the Mesolithic layers on Gotland have been characterised as belonging to the Maglemose culture, with the exception that microliths, which are connected to this culture, are rarely found on the island (Apel & Storå 2018:296pp). Microlith technology have been associated with hunting of non-volant mammals i.e. all land mammals except for bats (Zvelebil 2008). Besides hares, Gotland lacked land living mammals, and there would be little use for this technology on the island (Lindqvist & Possnert 1999). Gotland was covered in ice during the last glacial period (Andersen & Schack Pedersen 1998), and the island has not been connected to the mainland since that period (Svensson 1989; Liljegren & Lagerås 1993; Björck 1995), although this has sometimes been suggested (Munthe et al. 1925:68; Österholm 1989:25pp). Munthe et al. (1925) write that a land bridge between Gotland and the mainland was likely because this is the only possible explanation for the presence of zooarchaeological remains from wild animals on the island. They also consider that the boats used by Stone Age people were simply too small and inadequate to carry animals (Munthe et al. 1925:72). The idea of a land bridge was further discussed by Inger Österholm, who even hypothesised that some species could have evacuated Gotland as it was about to turn into an island (Österholm 1989:25), and that this would explain the finds of ancient skeletal remains from species which are no longer present on the island. Bornholm, another island in the Baltic Sea, was connected to mainland Germany by a land bridge (Björck 1995), which means that the fauna on this island looked very different to the fauna of Gotland, as it housed populations of moose, beaver, roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and wild boar (Casati & Sørensen 2009:248p).

The island of Gotland is located in the middle of the Baltic Sea, and the distance today to mainland Sweden is c. 80 km, c. 150 km to the Baltic countries and c. 230 km to the continent in the south. Because of Gotland's history and geographical location, few terrestrial mammalian species are represented on the island, and we have a fairly good idea of when the different species first

appeared. The majority of the wild animals arrived during the last 200 years, transported by humans, including Gotland's famous rabbit (*Oryctolagus cuniculus*) (Noréhn 1984; Lindqvist & Possnert 1997:70; Hedgren 2003). The first non-volant mammal on the island was a lagomorph, the mountain hare. Remains of this animal have been dated to the Mesolithic period between c. 7,529 and 6,906 BC (Lindqvist & Possnert 1997:40, 1999). Two other non-volant wild mammals were present on Gotland during the Stone Age, the red fox (*Vulpes vulpes*), which arrived c. 5,500 BC, some 2,000 years after the hare (Lindqvist & Possnert 1997:43), and the hedgehog (*Erinaceus europaeus*), whose earliest remains are dated to c. 2,700 BC. The latter is most likely to have been transported by humans in some way (Lindqvist & Possnert 1997:69; Fraser et al. 2012). Remains of hedgehogs are regularly found at Pitted Ware Culture sites on Gotland, both in graves and in cultural layers (Lindqvist & Possnert 1997:69). It is not impossible that the red fox was also translocated to Gotland by humans. This has been suggested on the basis of finds of very worn-down red fox teeth, which could indicate that the foxes were held in captivity (Lindqvist & Possnert 1999). There are also examples of how foxes were translocated by humans in prehistoric times (Collins 1991; Guislaine et al. 2000; Rick et al. 2009). The lack of non-volant mammals means that the reasons for settling on Gotland must be different from the reasons for settling on the mainland. Access to marine mammals is an obvious reason, judging from the zooarchaeological material from the early sites. More recently, the importance of freshwater fish has been highlighted, as well as avian and plant resources (Boethius et al. 2017; Apel & Storå 2020). The early sites on Gotland dating to 7,200–6,000 cal BC are located close to either inland lakes or the sea, predominately in northern parts of the island (Apel & Storå 2020).

## 4. Materials and methods

This chapter outlines the methods used in the thesis, as well as the methodology used at the most important archaeological sites mentioned in the thesis.

### 4.1 On DNA

DNA is composed of four nucleotides, the pyrimidines cytosine (C) and thymine (T) and the purines adenine (A) and guanine (G), arranged on a backbone of a phosphate group and a five-carbon sugar. These nucleotides are arranged in complementary strands held together by a hydrogen bond. (C) is complementary to (G) and (T) is complementary to (A), and the two strands are arranged in a double-helix formation (Freeland 2005:4p; Campbell 2008:86pp). The ends of the DNA strand differ from each other, and are therefore said to have a direction, running from 5' to 3'. As the two strands in a DNA molecule run in different directions, they are called antiparallel (Campbell 2008:88). The negatively charged DNA is wound around positively charged proteins called histones. This combination, known as chromatin, plays a key role in the packing of DNA, and is coiled together with chromosomes during some phases in the cell cycle (Campbell 2008:320).

The DNA strands contain the information that decides what occurs and what is produced in the cell, but DNA is also the hereditary material that organisms inherited from their parents. The DNA is arranged in units called genes which, through the process called gene expression, transcribe the DNA code into single-stranded ribonucleic acid (RNA), known as messenger RNA (mRNA). The RNA molecule is usually single stranded and has the same bases as DNA, except for the base (T), which is replaced by uracil (U) (Freeland 2005:4p). The mRNA leaves the cell nucleus and enters the ribosomes, where it is translated to amino acids with the help of transfer RNA (tRNA). The amino acids then bind together to form different proteins (Freeland 2005:4p; Campbell 2008:325pp). At the same location (locus), different genes (alleles) may occur, which can lead to the creation of a different set of amino acids. The nuclear genome in human cells comprises c. 3200 MB of DNA, which is the majority of the genetic material in an organism (Brown & Brown 2011:14). In humans, this DNA is divided into 24 chromosomes, of which 22

are autosomes and two are the sex chromosomes X and Y. Humans are diploid, which means that they have two pairs of each autosome and either two X or one X and one Y chromosome. During reproduction, one set of chromosomes is inherited from each parent. During meiosis, homologous chromosomes exchange genetic material with each other which will cause new combinations of genes. This exchange is called recombination (Freeland 2005:12p). Following a genetic lineage back in time is not as straightforward as a molecular marker which undergoes no recombination. For humans, the Y chromosome is only passed down on the paternal side, and only small parts of it undergo recombination (Freeland 2005:38p), making it easier to trace a genetic lineage back in time on the paternal side.

Another type is known as mitochondrial DNA (mtDNA), located in the mitochondrion, which is an organelle responsible for cellular respiration (Campbell 2008:109). This mtDNA is a circular DNA molecule that contains a number of genes as well as a non-coding region called the control region. This DNA molecule is considerably smaller than the DNA molecules in the nucleus; the mtDNA molecule for humans comprises only 16,569 bp (Brown & Brown 2011:14). The mtDNA has a number of properties which make it popular in population-genetics studies. Compared to nuclear DNA, mtDNA is uniparentally inherited and passed down on the mother's side, which means that it does not undergo recombination, making it easier to follow a genetic lineage through time (Freeland 2005:32pp). Another characteristic of mtDNA is that what it lacks in size, it makes up for in numbers. There are about 8,000 copies of mitochondria per cell, where nuclear DNA has only one copy per cell (Brown & Brown 2011:15). This means that analyses of mtDNA are more likely to succeed than those of nuclear DNA when the DNA source is degraded, and this has made it a popular marker in terms of working with aDNA. The mutation rate for some parts of mtDNA is higher than in protein-coding genes in the nucleus, and this makes it possible to follow several genetic lineages in the same population, another fact which means it has been widely used in population genetics (Freeland 2005:32p). Equally, since there has been extensive research on mtDNA, it has often been easy to find relevant DNA sequences for comparison in online gene databases. The popularity of mtDNA in aDNA analyses has nevertheless decreased as new methods have evolved which make it easier to analyse DNA from the nucleus, and this is more informative than the short mtDNA molecule.

#### 4.1.1 Ancient DNA

All macromolecules degrade over time, and DNA is no exception to this rule. DNA in living organisms differs from aDNA as there are repair processes in living organisms which are activated when the DNA is damaged (Lindahl 1993:709; Pääbo et al. 2004:646). For this reason, aDNA looks different to DNA in living organisms. One characteristic of aDNA is that strand breaks

cause the polynucleotide to be shorter, so it is usually not possible to obtain sequences longer than 200-300 BP from aDNA (Hummel 2003:73; Brown & Brown 2011:118). The DNA is degraded by a set of factors. After the death of an organism, digestive enzymes that have been isolated in the lysosomes break free and start to degrade biomolecules, including DNA. The DNA is also degraded by microorganisms, bacteria and fungi which break down the biomolecules in order to absorb them (Pääbo et al. 2004:646; Brown & Brown 2011:116). After this immediate onslaught, the DNA molecules are degraded by slower processes such as chemical and physical factors like hydrolysis and oxidation, which cause nucleotide changes and base- and sugar fragmentation (Pääbo et al. 2004:646). The environmental factors at the site where the organism was buried are the key to DNA survival (Keighley et al. 2021). For good preservation, the temperature should be low and stable, and humidity in the soil should also preferably be low. The pH value of the soil should be neutral or slightly alkaline, so that the bones and teeth, and consequently also the DNA, are preserved. Another important factor in DNA preservation involves the quantity of microorganisms at a site. If it is too high, the DNA can be totally destroyed. One last factor, especially important for material found at archaeological sites, is that it is removed from the condition in which it has been buried, and placed in new conditions that could initiate a new wave of DNA degradation (Burger et al. 1999:1722pp). Ancient DNA is not only degraded in length, but the amount of DNA left in ancient samples is also often minute compared to samples from modern organisms. This leads to a risk of contamination, another pitfall involved in working with aDNA. Degradation of DNA is inevitable with time, meaning that there is a time limit on how old a sample can be before the DNA is too degraded to be extracted and analysed. When studies in the field of aDNA were first established, before this was known, some research groups claimed to have successfully extracted DNA from samples that were up to 80 million years of age (Woodward et al. 1994; Cano & Borucki 1995). This was later proved to involve contamination, or was shown to be impossible to replicate (Zischler et al. 1995; Austin et al. 1997). Today the oldest reliable DNA comes from a mammoth tusk that has been dated to up to 1.2 million years ago (van der Valk et al. 2021).

## 4.2 Ancient DNA methodology

The field of aDNA is still relatively young, but has an eventful history, and the next section provides a short overview.

### 4.2.1 Short overview

The history of aDNA analysis began in China at the beginning of the 1980s, when a research group showed that DNA was preserved in human remains

from the Han dynasty (Hummel 2003:1). During the following years, aDNA studies were performed not only on humans, but also on various plant and animal species (Higuchi et al. 1984; Pääbo 1984, 1985; Johnson et al. 1985; Rogers et al. 1985). Although these studies were all ground-breaking, the real breakthrough in the field came with the introduction of the polymerase chain reaction (PCR) machine (Mullis & Fallona 1987; Hummel 2003:1). This allowed small amounts of DNA to be amplified, making it possible to analyse them. The next breakthrough in the field occurred at the end of 1980s, when DNA from bone material was amplified for the first time (Hagelberg et al. 1989). This advance proved especially feasible for archaeology, but also for other disciplines such as palaeoecology. Bones and teeth are the most common sources of aDNA, simply because they are such common find materials at archaeological excavation sites, and because DNA preserves well when it is contained in bones and teeth. Other sources, such as hair (Rasmussen et al. 2010), coprolites (Gilbert et al. 2008), eggshells (Oskam et al. 2012), bog bodies (Fricker et al. 1997), bones from mummies (Keller et al. 2012), permafrost cores (Willerslev et al. 1999), sediments (Willerslev et al. 2003), seeds and plant remains (Oliveira et al. 2012), have been used to obtain aDNA successfully (Brown & Brown 2011:91pp, 233).

#### 4.2.2 Applications of aDNA studies

Since DNA extracted from ancient samples is degraded, aDNA analyses have been limited to short sequences. Despite this, aDNA has been utilised in a wide range of applications such as kinship studies, species identification, sex determination, palaeopathology and population genetics (Brown & Brown 2011:150pp). The emergence of next-generation sequencing in aDNA studies has made the results more reliable, and has also improved the chances of obtaining new information from source material.

#### 4.2.3 PCR-based methods

After the introduction of the PCR as a necessary tool for developing the aDNA field, PCR-based methods were favoured for 20 years until other methods took over. Since only minute amounts of DNA are found in ancient material, it has to be amplified if it is to be analysed. Before running a PCR, small oligonucleotides called primers are created. These are the starting point for synthesising the DNA. They can be designed from known DNA sequences which can be found in gene databases, and should be designed to be both site and species-specific. The primers should be around 20-25 bp to be specific. The total sequence, including primers, is usually less than 200 bp, but the target sequence can be several times longer than this. The problem can be solved using overlapping primers which are run in different PCRs. The downside of this method is that it consumes considerable DNA extract.

An approach is used which mimics the way cells transcribe DNA, by adding the enzyme taq polymerase, nucleotides and primers to the DNA extract. During the first step in a PCR cycle, denaturation, the temperature is raised to 94°C, causing the hydrogen bonds in the double-stranded DNA to be released and the segment to open into single-stranded DNA. During the next step, annealing, the temperature is lowered to 50-65°C, binding the primers to their designated area. The last step is elongation, where the temperature is raised to 72°C, causing the DNA-polymerase to start to build on the DNA template, using the primer as a starting point (Brown & Brown 2011:26pp). The PCR is a very powerful tool, doubling the number of molecules in the DNA in each cycle. The success of the PCR is then controlled using agarose gel electrophoresis, which separates the DNA molecules according to size by using an electric current. The negatively charged DNA molecules travel towards the positive pool, and the size of the DNA product can then be compared to produce DNA ladders of known size which have been added to the agarose gel. The DNA amplicons are visualised using ultraviolet light, and can then be cleaned and sent to be sequenced.

The DNA sequencing step enables the nucleotide sequence to be determined. The most widely used method in aDNA research in the first two decades was known as Sanger sequencing. This process is similar to PCR, with the difference that only one primer is used. Another way in which it differs from PCR is that, in addition to dNTP, a mix of dideoxynucleotides (ddNTP) is added. The ddNTPs are similar to dNTPs but lack an OH group, which causes the synthesis to halt when it binds to the DNA template (Free-land 2005:23p; Campbell 2008:408p). Since the ddNTP binds at random, fragments of different lengths are created. The ddNTP is dyed so that nucleotides located at different positions of the sequence can be determined (Brown & Brown 2011:30p).

#### 4.2.4 Next-generation sequencing

The introduction of next-generation sequencing methodology (NGS) made it possible to sequence hundreds of thousands of sequences per run, instead of the small sequences which are the usual outcome of PCR-based methods (Millar et al. 2008; Brown & Brown 2011:33p). This method uses short sequences, the usual sequence size varying between 10 and 100 bp. The typical characteristics of aDNA with short sequences, which were previously seen as a disadvantage, became an advantage with the introduction of the high-throughput DNA-sequencing methodology. Next-generation sequencing requires DNA libraries to be built. For this thesis, double-stranded DNA libraries were created using the protocol by Meyer & Kircher (2010), which involves the following steps. In the *blunt-end repair* step, the 5' - and 3' ends are repaired or removed. In the next step, known as *adapter ligation*, adapters are linked to both the 5' - and 3' end of the repaired DNA strand. The adapters only link single-stranded



sequences, and are therefore complemented in the next step, known as *fill in*. The DNA libraries are attributed to an individual index which, together with adapters, is attached to the DNA libraries using a thermal cycler (Meyer & Kircher 2010). This new method was a game changer for the field, and made new research questions possible. The massive quantity of data generated, however, led to completely new challenges.

#### 4.2.5 Reference sequences

A problem following the shift from PCR-based to NGS methods involves the lack of reference material. In **Paper II**, for example, previous studies of the Baltic grey seal only targeted a partial mitochondrial sequence, which meant that we needed to crop our ancient full mitochondrial sequences to that size. Another problem we encountered was the absence of published annotated genomes in online gene banks. Annotated genomes are sorted into genes and chromosomes, and are necessary for mapping the data sets derived from the high-throughput shotgun-sequencing methods used in this thesis. The first annotated genomes created were from humans and for domesticated mammals with a high economic value. The lack of annotated genomes for pinnipeds led to the novel solution presented in **Paper V**, where genomic sex identification was performed on our data sets by mapping them against a dog genome. Since females have two X chromosomes and males only one, the relative number of reads mapped to the X chromosome will be higher for females than for males. This method was used for identifying grey seals by sex in **Paper II** and moose in **Paper III**. The absence of annotated genomes also caused problems for the moose study in **Paper III**. A project to create a de-novo genome was therefore initiated (Dussex et al. 2020).

#### 4.2.6 Pitfalls

The characteristics of aDNA affect the way it can and should be processed and analysed. Degradation of the DNA can lead to misinterpretations of the data, and the minute amount of DNA that remains in ancient samples can be so contaminated by modern DNA that the endogenous aDNA may be hard to distinguish. The risk of contamination is greater when working with ancient human material than when working with ancient faunal material, but should still not be overlooked (Gilbert et al. 2005). There are at least five ways in which contamination can find its way into a DNA extract or PCR product. The first two occur when the organism is handled after death and when the organism is deposited in the ground. These are aspects which the researcher cannot control. The third source of contamination involves handling by the excavating archaeologist, the osteologist or the museum curator, and this source of contamination can be avoided if the whole excavation and subsequent analysis chain is aware of contamination and takes actions to prevent it (Brown &

Brown, 2011:138pp). This, however, is often hard to control in analysing museum specimens which were excavated a long time ago, as there is often no way of telling how much a museum specimen has been handled and by whom. The last two sources of contamination occur in the laboratory environment, where cross contamination can take place with old PCR products and reagents, and with lab material that has been contaminated (Brown & Brown 2011:138pp). The contamination issue provoked a crisis in the field of aDNA in the latter half of the 1990s and the beginning of the 2000s, and led to the development of a list of criteria to follow in working with degraded DNA (Cooper & Poinar 2000). The criteria are as follows:

1. Work in a physically isolated area in a room dedicated for the purpose.
2. Use negative control extractions and amplifications.
3. The PCR products must look ancient, and cannot be too long.
4. The results should be able to be reproduced with multiple extracts and PCRs.
5. The products should be cloned.
6. A different research group should replicate the result independently.
7. The sample used for extraction should be well-preserved.
8. The number of aDNA copies should be quantified.
9. Associated remains should be examined to see if they are well-preserved or show signs of contamination.

In addition, different methods of removing contamination in bone or teeth have been utilised, such as treating the sample with bleach, ultraviolet irradiation in spectrolinker or removing the outer surface, since the contamination is often shallow (Brown & Brown 2011:140pp). As Gilbert et al. (2005) suggest, the criteria for working with DNA are rarely followed to the letter, and this should not be necessary in every case if the researcher can satisfy the reader that the result is authentic. The lab work for this thesis was performed in dedicated aDNA facilities, with separate rooms for drilling skeletal remains, extracting DNA, library building, extracting collagen and post-PCR work. With the introduction of high-throughput sequencing technology in the aDNA field, endogenous DNA can be distinguished and isolated from contaminating modern DNA using a statistical framework that recognises the damage pattern characteristic of aDNA (Skoglund et al. 2014).

### 4.3 Archaeological sites

The zoological material analysed in this thesis derives from a large number of archaeological sites in various geographical regions and time periods. Information on the sites is provided in Table 1 and Fig. 2. Here, the two sites which have provided the majority of the samples, Stora Förvar and Bastuloken, are presented in detail, as they have a special place in the thesis.

*Table 1. Sites from which samples were analysed in this thesis. Both successful and unsuccessful samples are included. Meso=Mesolithic period, Neo=Neolithic period, BA=Bronze Age, IA=Iron Age and MP=Medieval period.*

Site	Country	period	papers	Map id
Advik	Norway	Neo	IV, V	1
Bergeby	Norway	Neo	IV, V	2
Gressbakken	Norway	Neo	IV, V	3
Gropbakkeengen	Norway	Neo	V	4
Mortensnes	Norway	Neo	V	5
Agnsjön	Sweden	Neo	III	6
Bastuloken	Sweden	Neo	III	7
Tåsjö	Sweden	Neo	III	8
Brömsängsbacken	Åland	IA	IV, V	9
Jettböle	Åland	Neo	IV, V	10
Kattby	Åland	IA	IV, V	11
Åsgårda	Åland	Neo	V	12
Åloppe	Sweden	Neo	I	13
Dafter	Sweden	Neo	I	14
Rörvik	Sweden	Neo	I	15
Brunn	Sweden	Neo	IV, V	16
Jordbrobopplatsen	Sweden	Neo	I	17
Korsnäs	Sweden	Neo	I, IV, V	18
Motala/Strandvägen	Sweden	Meso	I	19
Frälsegården	Sweden	Neo	I	20
Alvastra	Sweden	Neo	I	21
Scheelegatan	Sweden	Neo	I	22
Ajvide	Sweden	Neo	IV, V	23
Gisslause	Sweden	Meso	I	24
Hemmor	Sweden	Neo	IV, V	25
Ire	Sweden	Neo	I	26
Lilla Hultungs	Sweden	MP	I	27

Lilla Sojvide	Sweden	IA	I	28
Stora Förvar	Sweden	Meso, Neo, BA, IA	I, II, IV, V	29
Strå	Sweden	Meso	I	30
Uddvide	Sweden	IA	I	31
Visborgs Kungsladugård	Sweden	Meso	I	32
Västerbjers	Sweden	Neo	I	33
Asva	Estonia	BA	IV	34
Gåtebo	Sweden	Neo	I	35
Köpingsvik	Sweden	Neo	I	36
Mysinge	Sweden	Neo	I	37
Bökebergsslätt	Sweden	Neo	I	38
Hindbygården	Sweden	Neo	I	39
Kvärlöf	Sweden	Neo	I	40
Östra Vemmenhög	Sweden	Neo	I	41
Šventoji 23	Lithuania	Neo	I	42
Argusgrunden	Denmark	BA	IV	43
Flynderhage	Denmark	Meso/Neo	IV	44
Gudumlund	Denmark	Neo	IV	45
Krabbesholm	Denmark	Neo	IV	46
Aabenraa	Denmark	BA/IA	IV	47
Ronæs skov	Denmark	Meso/Neo	IV	48
Neustadt	Germany	Meso/Neo	II, IV, V	49
North Sea	The Netherlands	Unknown	V	-
Qeqertasussuk	Greenland	Neo/BA	IV	-

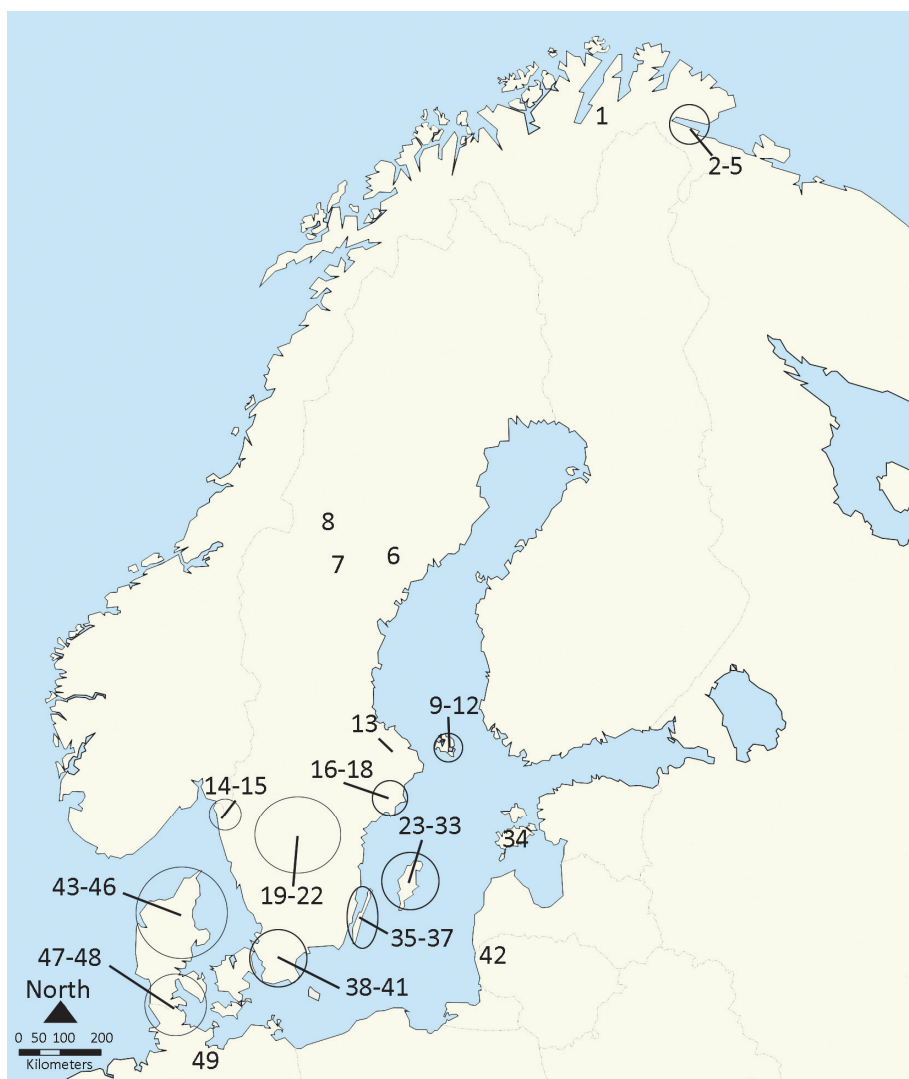


Figure 2. Map of sample location. For description, see Table 1. Not included in the map are samples from the coast of the Netherlands and Qeqertasussuk, Greenland.

#### 4.3.1 Stora Förvar

The island of Stora Karlsö is situated 6.5 km west of Gotland and has an area of 2.5 km<sup>2</sup>. The island consists of limestone bedrock which has proved to be very beneficial in preserving bones and DNA. The Stora Förvar cave was excavated between 1888 and 1893 by Hjalmar Stolpe and Lars Kolmodin (Schnittger & Rydh 1940:20). The cave was divided into sections of various sizes, labelled A-I, and excavated in 30 cm spits (Fig. 3).

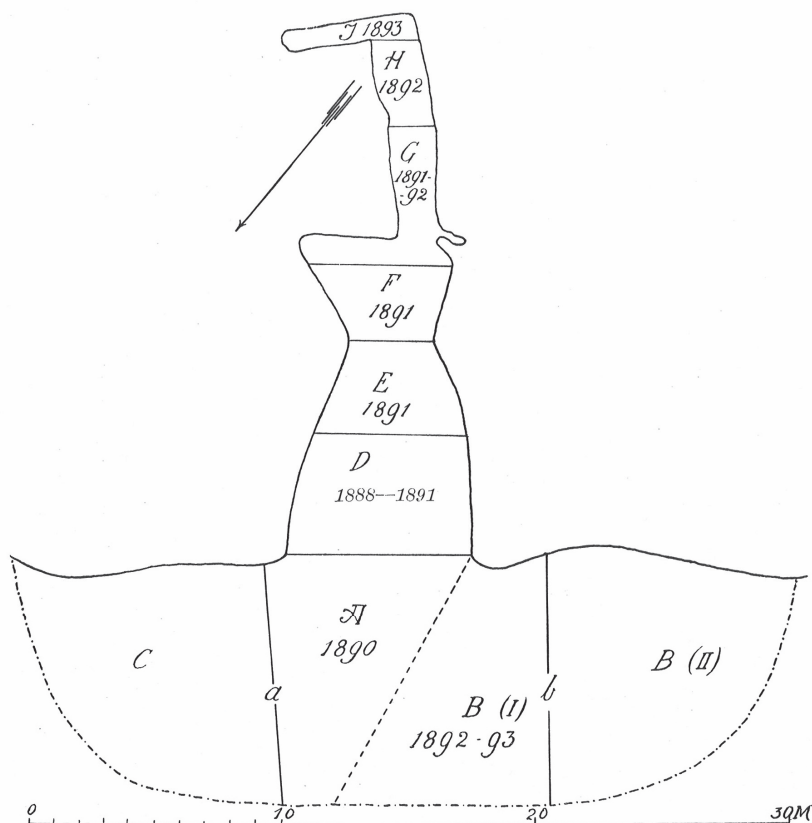


Figure 3. Plan of the sections in the Stora Förvar cave and the year of excavation. From Schnittger & Rydh 1940:23.

The cultural layers were up to 4.5 meters thick and have been accumulating from the Mesolithic Period until the cave was excavated, except for an interruption of approximately 1,400–2,000 years in the sequence from c. 6,000 cal BC to 4,000 cal BC (Apel et al. 2018; Apel & Storå 2020). As seen in Fig. 4, the stratigraphic cross section of the cave is sloping which means that the spits in the different sections are not directly compatible.

The original excavators never completed the excavation report, and it was not until 1940 that Hanna Rydh and Bror Schnittger published it in full (Schnittger & Rydh 1940). Unfortunately, they did not participate in the excavation themselves. The enormous quantities of zooarchaeological remains collected during the excavation have never been thoroughly analysed or published in full, but several separate studies have been published where parts of the cave have been analysed, e.g. Pira (1926), Ericson & Knape (1991), Lindqvist & Possnert (1997, 1999), Apel & Storå, (2018, 2020), Günther et al. (2018).

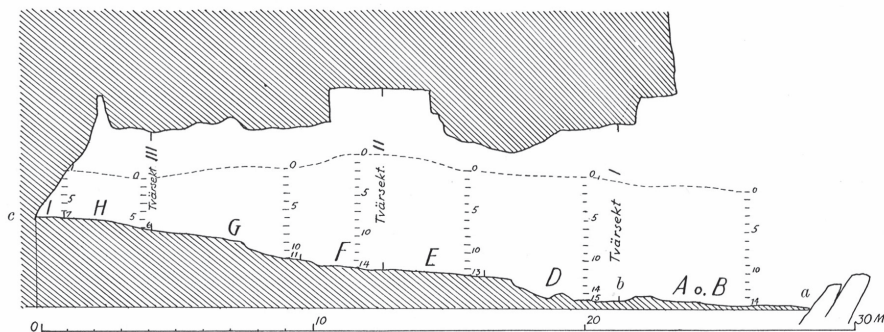
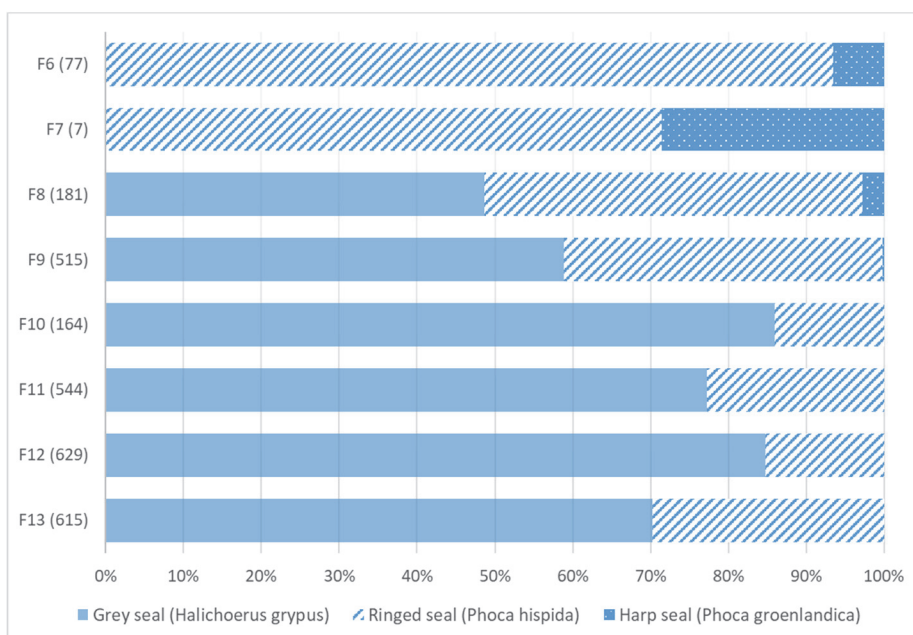


Figure 4. The stratigraphic cross section of the Stora Förvar cave showing the different sections and spits. The dotted line marks the level of the cultural layer prior to excavation. From Schnittger & Rydh 1940, p 62.

The Mesolithic layers are dominated by bones from marine mammals (Pira 1926; Lindqvist & Possnert 1999; Apel & Storå 2018:283p). The zooarchaeological material shows that the frequency of different seal species changes with time. Although the earlier layers are dominated by grey seal, the ringed seal gradually becomes more abundant and the harp seal starts to appear after the hiatus (Fig 5). The majority of grey seals in the Mesolithic layers of the cave are cubs and sub-adults (Apel & Storå 2018:289p). For this reason, it has been suggested that the island of Stora Karlsö housed a breeding colony of grey seals during the Mesolithic period (Lindqvist & Possnert 1999). Another possibility is that breeding took place on the ice in the proximity of the island. The grey seal then disappeared from the cave at the end of the Mesolithic period, and when it returned, harpoons had become more common among the artefacts found, indicating a change in hunting technique. Hunting with harpoons was probably not a common hunting method before the hiatus (Apel & Storå 2020). There are few remains of waste material from the production of bone tools in the Mesolithic layers in the cave, but the bone tools found from before the hiatus are made from seal bones (Apel & Storå 2020). Local material was used for both stone and bone tool production (Apel & Storå 2018:296pp, 2020).



*Figure 5. The frequency of different seal species in section F13-F6, where F13 is the oldest layer. Number of specimens in brackets. Modified from Apel & Storå 2018:288.*

### 4.3.2 Bastuloken

Several small research excavations have been undertaken at the Neolithic site of Bastuloken, located on the shore of a bog in Västernorrlands län, northern Sweden (Fig. 2). The site contains four embanked sites, and several systems of pitfall traps are found in the area, on both sides of the river Vängelälven (Fig. 6). Some 300 metres from the site is a rock painting depicting moose, which was found in 2003 (Lindgren 2004).



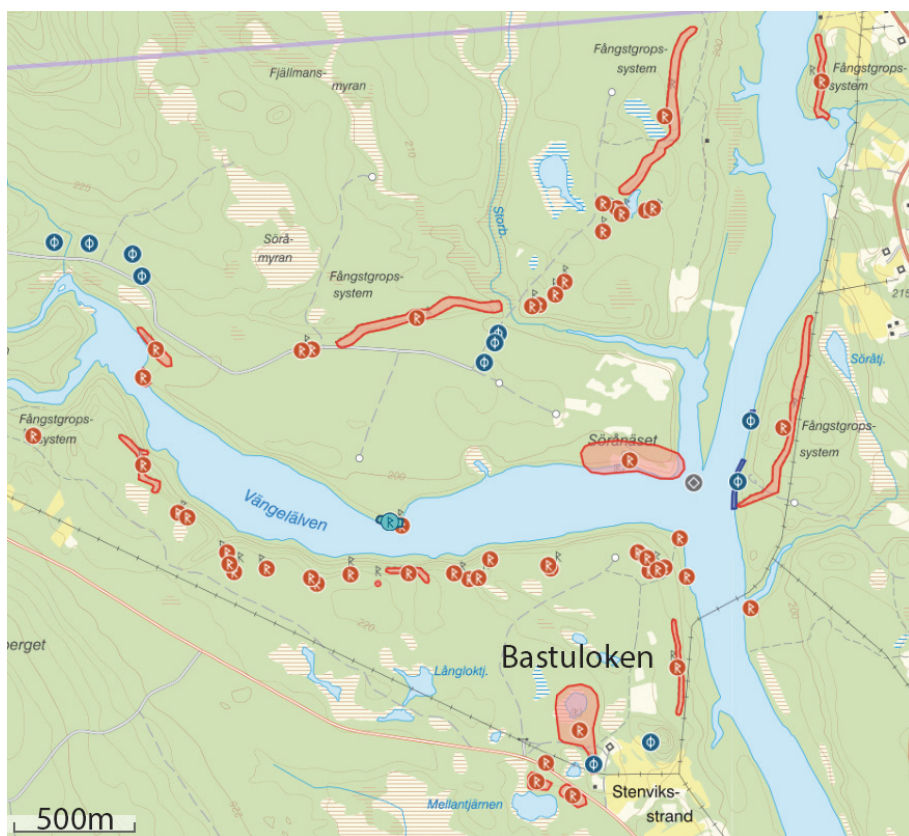


Figure 6. The Neolithic site near the Bastuloken bog, with several systems of pitfall traps (Sv. Fångstgropar) visible in close proximity to the site (Raä, Fornsök).

An initial excavation of the site in 2005 revealed vast numbers of well preserved and unburnt moose bones (Engelmark & Harju 2007), which is uncommon in northern Sweden. Two research excavations took place in 2009 and 2010, with the aim of recovering moose bones from as many individuals as possible to build a chronology of the site (Larsson 2009, 2010a). The intention was that the moose bones could be used to study morphologic and genetic changes in moose during the time the site was utilised. A total of 9 m<sup>2</sup> was excavated during 2005, 2009 and 2010 in one of the four embanked settlements, in square pits of 1m<sup>2</sup> and in spits of 10 cm (Fig. 7). The excavations revealed c. 35 kg of unburnt bone and 350 g of burnt bone, as well as several hundred litres of fire-cracked stone. The osteological report showed that the majority of bones derived from moose, but other species such as the European pine marten (*Martes martes*), beaver and various bird and fish species were also found (Storå et al. 2011).

Radiocarbon data show that the site was used between 2,500 and 1,800 cal BC, but the most intensive period of utilisation seems to have been between

2,500 and 2,300 cal BC (Larsson 2010b). The quantities of moose bones decrease in the centuries that followed until the site was abandoned.

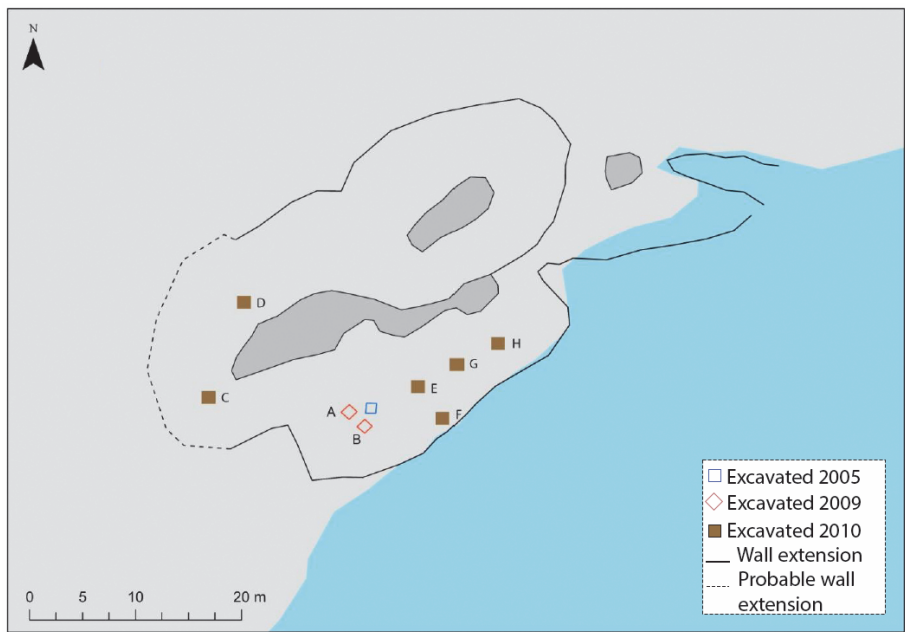


Figure 7. Excavated areas in Bastuloken, (modified from Larsson 2010a, initial map by Ronny Smeds, Västerbottens Museum).

## 5. Case studies on prehistoric human impact

### 5.1 Animal translocations: Mountain hare

The mountain hare (Fig. 8) has been present in Central Europe since the last glacial period (Kurtén 1968; Corbet 1986; Angerbjörn & Flux 1995), and spread to the north as the ice retreated, eventually reaching Fennoscandia some 10,000 years ago (Kurtén 1968; Lepiksaar 1986; Thulin 2003). The physically tough mountain hare was among the first larger terrestrial species to enter deglaciated areas (Thulin et al. 1997). Relict populations of mountain hare are present in the Alps, eastern Poland, Scotland and Ireland, but the current distribution of this species is mainly in northern latitudes stretching from Fennoscandia to Japan (Kurtén 1968; Angerbjörn & Flux 1995; Thulin 2003).

The mountain hare mainly inhabits mixed forests and tundra, where it feeds on grass, twigs, leaves, moss, bark and lichens (Kurtén 1968:230; Angerbjörn & Flux 1995). The breeding season starts in spring, and annual recruitment involves 1-3 litters/female. The mountain hare is a prey species for a number of predators such as the red fox, wolf (*Canis lupus*), wolverine (*Gulo gulo*), lynx (*Lynx lynx*), European pine marten, mink (*Mustela vison*), stoat (*Mustela erminea*), several birds of prey and owls (Angerbjörn & Flux 1995). The present distribution of mountain hares in Sweden is north of 59°N, and on the islands Öland and Gotland in the Baltic Sea (Angerbjörn & Flux 1995). Because of the history and geographical location of Gotland, the occurrence of mountain hares on the island is rather enigmatic (see chapter 3.3), particularly as skeletal remains of mountain hares show that they were already present during the Mesolithic period. **Paper I** takes its starting point from three main questions. Firstly, what was the origin of the mountain hares on Gotland? Secondly, were the early hares on Gotland related to later populations on the island? Thirdly, how did the hares reach the island?



Figure 8. Mountain hare on Stora Karlsö with the islands of Lilla Karlsö and Gotland in the background. Photo by the author.

To answer this, skeletal material from a total of 83 individual mountain hares was genetically analysed, dating from the Mesolithic period to the 19<sup>th</sup> century, from eight sites on Gotland, 18 sites on the Swedish mainland and one site in Lithuania. This was then compared to previously published haplotypes from modern and ancient hares from different locations in Eurasia, from Ireland in the west to eastern Siberia, and to the Don hare (*Lepus tanaiticus*) morphotype (Melo-Ferreira et al. 2007; Prost et al. 2010).

A total of 46 out of the 83 hare samples yielded enough endogenous DNA for amplification and sequencing. The results show a discrepancy between the samples, creating two different genetic groups on Gotland that were present on the island on different occasions. The first group was present during the Mesolithic period, the oldest sample dating to 7,304–6,833 cal BC, but this then disappeared from the island around 6,208 – 5,989 cal BC. The mountain hare then remained absent until 2,848–2,471 cal BC, when it reappeared in the zooarchaeological record and remains there today. The Mesolithic haplotypes are no longer found among these hares. Instead, new haplotypes appear, not previously found on the island. This shows that the mountain hare became extinct on Gotland during the Mesolithic. Furthermore, it suggests that the species was introduced to the island on at least two separate occasions. The

reason why the hare was extirpated during the Mesolithic is not fully understood, but several events which coincide with its disappearance could have contributed to the decline of the hare population. For example, one of the most pronounced environmental events, the 8.2k cold event, coincides with the time that mountain hares disappeared from the island. Furthermore, a new species, the red fox, appeared on the island, and may have further contributed to the decline of the mountain hare population. Finally, the *Littorina* transgressions, which caused a loss of habitat, occurred around the same period. Another factor, which has not yet been studied, involves inbreeding.

The origin of the Mesolithic group of hares is not clear. These hares are genetically close to both modern hares from eastern Siberia and modern hare populations in Scotland. The modern hare population in Scotland is a relict population from the last glacial period (Angerbjörn & Flux 1995). This probably means that the Mesolithic hares from Gotland and the modern hare populations from eastern Siberia and Scotland derive from a common refugium which existed south of the ice rim during the last glaciations. The hares in the second group, which arrived on Gotland 2,848–2,471 cal BC, are genetically close to contemporary hares from the Swedish mainland, which means that they are most likely to have derived from mainland Sweden. Given the isolated location of the island, it seems highly unlikely that the hares managed to travel the distance to Gotland and found a breeding population on two occasions, which explains the lack of other non-volant mammals on the island. Equally, the strong site fidelity of mountain hares in general and female mountain hares in particular (Dahl & Willebrand 2005) makes it highly unlikely that they managed to migrate to Gotland by themselves. On the contrary, the study suggests that the hares are most likely to have reached the island through human-mediated transport. There are several other examples of the translocation of hares in prehistory (Kasapidis et al. 2005; Suchentrunk et al. 2006; Mengoni et al. 2018). If hares were indeed translocated to Gotland, this would be an example of an early alteration in a wild-animal population in Scandinavia. The hares in the second group are most likely to have derived from the Swedish mainland, which is an indication of contact between the mainland and Gotland during the Neolithic period. The fact that people brought wild animals to Gotland during the Neolithic period corresponds to a hedgehog study on the island, which showed that these animals were also brought to Gotland by people and had a western origin (Fraser et al. 2012). Another wild mammal that were brought to Gotland during the Neolithic includes the wild boar, as indicated by the numerous finds of this species in Pitted Ware Culture contexts.

As discussed in chapter 2.1.2, these examples would be neither the first nor the only translocation of wild animals in prehistory. The purpose of translocation is nevertheless difficult to ascertain. When the first humans arrived on Gotland, they met a landscape lacking in terrestrial animals, and had to depend on marine, avian and to some extent plant resources in order to survive. Under

these circumstances, it is plausible that hares were intentionally moved to the island in order to fuel and compliment the food sources, or because people had use for the fur. The hare bones discovered at Mesolithic sites are exclusively found in the refuse material from settlements, and do not indicate that the animals were treated in any way differently to other zoological remains from these sites.

Hares are easy to catch and transport alive, which makes them suitable for translocations. There are modern examples where leverets are caught and raised in captivity for later transport (Suchentrunk et al. 2006). Another explanation could be that hares were brought to the island by settlers in order to make the new environment more familiar. This practice of settlers introducing plants and animals to a new site as part of a transported landscape has been described by Patrick Kirch (Kirch 1982).

When the hares appeared once again on the island during the Neolithic period after a long absence, the situation on Gotland was very different in terms of fauna. Animals such as cattle, wild boar and sheep/goats had been introduced (Lindqvist & Possnert 1997:79). It was also during this period that the hedgehog was translocated to Gotland (Fraser et al. 2012). The island was now populated by people of the Pitted Ware Culture, whose subsistence had a marine focus with settlements close to the coast. The refuse material is often dominated by bones from seals and fish, but also wild boar (Österholm 1997). Isotopic analysis on human skeletal material in graves from the Pitted Ware Culture sites Vesterbjers and Ajvide shows that meat from wild boar only contributed very slightly to the diet (Eriksson 2004; Howcroft et al. 2014). The value of the hare as a food resource would have been less significant during this period, as domesticated fauna was available, and this indicates that the hares had a significance beyond their value as a food supply. Hare feet, for example, are a recurring feature in graves at Pitted Ware Culture sites during the middle Neolithic on Gotland, primarily the bones from the hind feet (Ahlström 2009). Hare feet were used as a lucky charm in Anglo-Saxon folklore (Ahlström 2009). In graves where other animal species have been placed as grave goods, e.g. wild boar, seal or hedgehog, the skulls and teeth were the preferred parts (Österholm 1997). Although the Anglo-Saxon meaning cannot be applied to Neolithic society on Gotland, it is possible that hare bones had some specific symbolic importance for this hunter-gatherer society.

The study shows that genetic analyses on faunal remains can contribute to knowledge on both human-animal relations during the Stone Age in Scandinavia and on the history of hare populations in prehistoric times. Translocation of hares and other living wild animals to new locations indicates a sense of long-term planning, a strategy involving returning to the same location a number of times to make use of the resource. Alternatively, it could be a sign of sedentary living. Thus, knowledge about wild-animal species in prehistory can be used to trace how humans travelled and acted during the period.



## 5.2 Hunting

### 5.2.1 Grey seal

The current global distribution of grey seal (Fig. 9) involves eastern Canada, the Baltic Sea, Iceland, all along the Norwegian coast, the north of the Kola Peninsula and the British Isles, including Ireland (Hall & Russell 2018:420p).  $^{14}\text{C}$ -dating shows that grey seals arrived in the Baltic Sea more than 9,000 years ago (Lindqvist & Possnert 1997:41, 1999; Pettersson & Wikell 2013). This would place their arrival in the Initial Littorina Sea at a point where there was a connection to the Atlantic Sea through the Danish Strait, but salinity in the Initial Littorina Sea at this time was very low (Berglund et al. 2005). It has also been hypothesised that the grey seal entered the Baltic basin through the Närke Strait in the middle of Sweden as early as the Yoldia Sea stage (Lindqvist & Possnert 1997:41), but this has been questioned by others (Lepiksaar 1986). The oldest Baltic grey seal in this study is dated to 7,453–7,275 cal BC, which is within the Initial Littorina Sea phase (Berglund et al. 2005). The distribution of grey seals during the Mesolithic period mainly includes the southern and central parts of the Initial Littorina Sea (Lindqvist & Possnert 1997:41), while the species was uncommon in the northern parts (Ukkonen 2002; Sommer and Benecke 2003).



*Figure 9. Image of grey seals, Helgoland, Germany. Photo by Aikaterini Glykou.*

The grey seal breeds on ice or on land on islands, and pupping in the Baltic Sea occurs from February to March, when pregnant females give birth to one pup weighing 10–20 kg (Hall & Russell 2018:422). After birth there is a lactation period for 18 days, followed by a post-weaning fast that lasts for 21 days on average, during which the pup does not enter the water (Hall & Russell 2018:420).

Grey seals have a capacity for long dispersal, but generally stay in the vicinity of certain haul-outs in the Baltic Sea (Sjöberg & Ball 2000, Karlsson et al. 2005; Oksanen et al. 2014). They often return to their previous pupping sites in areas where they breed on land (Pomeroy et al. 1994). Male juveniles move over larger areas than other groups in the population (Karlsson et al. 2005). Two subspecies of modern grey seal have been recognised on the basis of morphological, behavioural and genetic data: the Baltic grey seal (*Halichoerus grypus grypus*) and the Atlantic grey seal (*Halichoerus grypus atlantica*) (Berta & Churchill 2012; Graves et al. 2009; Klimova et al. 2014; Fietz et al. 2016; Olsen et al. 2018).

Grey seals show strong sexual dimorphism, where the males are considerably larger (170–310 kg) than the females (100–190 kg) (Hall & Russell 2018:422). Baltic Sea grey seals are top predators, and feed on a number of fish species such as herring (*Clupea harengus*), whitefish (*Coregonus lavaretus*), sprat (*Sprattus sprattus*), Cyprinids (Cyprinidae), salmon (*Salmo salar*), eelpout (*Zoarces viviparus*) and flounder (*Platichthys flesus*), but there are some regional differences within the grey seal population in the Baltic Sea (Lundström et al. 2013).

The Baltic grey seal population was close to extinction in the 20<sup>th</sup> century. Due to intensive hunting and pollution, the population had decreased from 80,000–100,000 by the beginning of the 20<sup>th</sup> century, and was down to 3,000 by the 1970s (Harding et al. 2007; Helcom 2018). Today the Baltic grey-seal population consists of more than 30,000 individuals (Helcom 2018). In **Paper II** we analysed the temporal genetic structure of the grey seal population in the Baltic Sea to see if it had been genetically continuous since it first appeared there during the Mesolithic period. A total of 69 ancient grey seals were analysed from the Baltic Sea, deriving from two main sites: the Stora Förvar cave in Sweden (n=63), dating from the Mesolithic period (c. 8,300–4,000 cal BC) to the Bronze Age and Iron Age (c. 1,700 cal BC – c. cal AD 1,050), and Neustadt in Germany (n = 6), dating to the late Mesolithic/early Neolithic Period (4,400–3,800 cal BC). The main material derives from the Stora Förvar cave because of the long human occupation of the site, with datings from the Mesolithic period until today, except for an almost 2,000 year-long hiatus where the cave was not utilised (Lindqvist & Possnert 1999; Apel et al. 2018; Apel & Storå 2020). The grey seal disappears from Stora Förvar at the end of the Mesolithic period, and is then replaced by ringed seal and harp seal in the



archaeological layers. It has been suggested that the large number of grey seal bones and the fact that grey seals disappeared are due to overexploitation which led to local extinction of the grey seal population (Pira 1926:130p).

The results from the radiocarbon dating show that Mesolithic grey seal hunting on Stora Karlsö took place between 7,453 and 7,275 cal BC, and between 6,942 and 6,625 cal BC. It was most intensive between 7,100 and 6,800 cal BC. The grey seal then disappears from this site and reappears again in the younger layers dated from 1,123–883 cal BC to cal AD 675–844. The grey seal is rare in the Baltic Sea during the intermediate period, but is found, for example at sites like Neustadt. The  $\delta^{13}\text{C}$  values of the Mesolithic grey seals from Stora Karlsö indicate that they lived in brackish or fresh water environments, with the exception of two individuals which showed clear marine values.

The temporal genetic structure of the Baltic grey seal reveals that the Mesolithic Stora Förvar samples are genetically different from the other samples. The temporal network (Fig. 10) shows that the majority of the Mesolithic Stora Förvar and Neustadt haplotypes have been lost and are not found in the historic and modern dataset. It equally shows that only two of the haplotypes found in the Mesolithic samples from Stora Förvar and the Neolithic samples from Neustadt are also found in the historic and modern samples. Two haplotypes from the Mesolithic Stora Förvar samples are also found in the Neustadt samples, dated to 4,566–4,056 cal BC, which indicates some continuity from the Mesolithic Stora Förvar population into the Neustadt samples.

Grey seals disappeared from the Stora Förvar site around 6,942–6,625 cal BC, and became rare in the entire Baltic following that period. The loss of haplotypes between the Mesolithic grey seals from Stora Förvar and grey seals from succeeding periods indicates that the grey seal population around Gotland went through a bottleneck. This is further supported by the fact that the Mesolithic grey seal population is genetically differentiated from both the grey seals from Neustadt and the Bronze Age and Iron Age samples from Stora Förvar. The reason for this bottleneck is not clear. The disappearance of the Mesolithic grey seal population on Stora Karlsö coincides fairly well with the Littorina transgressions, which could have caused habitat loss for grey seals in the area (Lindqvist & Possnert 1999). The first Littorina transgression was not a major climatic event in terms of a rise in sea level (Berglund et al. 2005). The influx of saline water that followed this event could potentially have affected primary production in the Baltic basin. It is known that environmental changes, and the trophic bottom-up effect that can follow when the abundance of a species is regulated by its resources (Townsend et al. 2008:312), can be more important than hunting in terms of regulating marine populations (Baylis et al. 2015). The most important prey for grey seals is herring, and the quality of the prey not only has an impact on grey seal reproduction but also plays a role in the first-year survival of the pups (Kauhala et al. 2017). The idea that

the *Littorina* transgressions caused these kinds of bottom-up effect cannot be totally excluded, but we found no evidence supporting this.

Despite the disappearance of the grey seal from Stora Förvar, radiocarbon data on other species show that the cave was utilised by humans for another 500 years after the grey seals disappeared from the site. The cave was utilised by humans until the 8.2k event which marked the end of Mesolithic human utilisation of the Stora Förvar cave (Apel & et al. 2018). People seem to have learned to cope with a situation where the grey seal was absent, and they survived by hunting other species during this last phase of occupation. Despite the new environmental conditions, there are no signs of a change in hunting technique during this period, as harpoons did not become common in Stora Förvar until after the hiatus (Apel & Storå 2020). The grey seal skulls found on the Neustadt site were extensively fragmented compared to the harp seal skulls found on that site, which indicate that the former was killed with a hit in the head with a club (Glykou 2013).

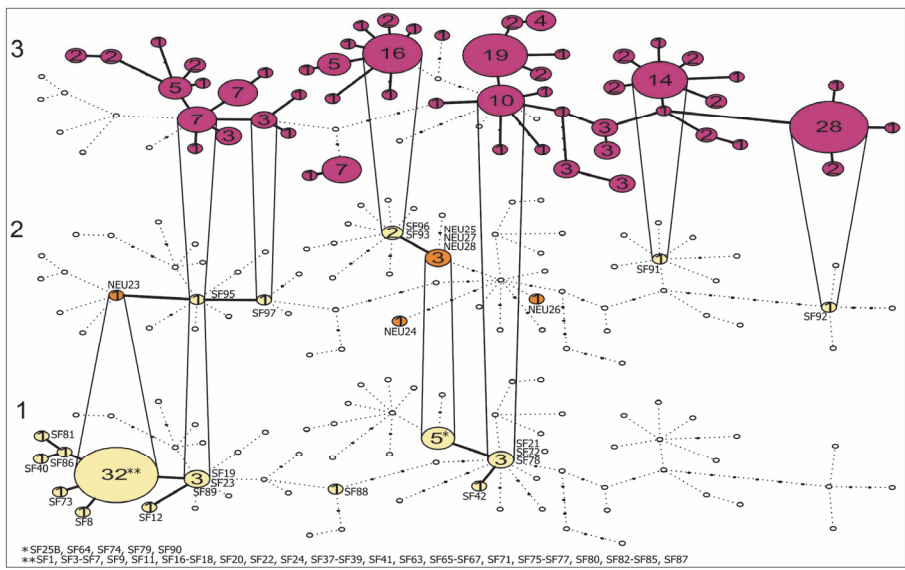


Figure 10. Grey seal haplotypes visualised in a temporal network, showing the genetic relationship between the ancient and historic/modern grey seals in the Baltic Sea. 1. Stora Förvar Mesolithic; 2. Neustadt and Stora Förvar Bronze Age/Iron Age; and 3. Historic/modern Baltic grey seals from Fietz et al. (2016). The black dots are missing haplotypes, and the white circles are haplotypes which are missing from that particular phase but found in others. Yellow = Stora Förvar, orange = Neustadt, purple = Baltic Sea historic/modern.

It is known from previous studies that grey seal pups and sub-adults were the main prey during the Mesolithic in Stora Förvar (Apel & Storå 2018:289). The high proportion of young seals also shows that hunting took place near a breeding colony and at least partly during the breeding period. The pups' unwillingness to enter the water during the weaning and post-weaning fast makes them vulnerable to hunting (Bennet et al. 2007). Additionally, grey seal pups have white fur, which could have made them desirable for prehistoric hunters (Apel & Storå 2018:295). Osteoarchaeological analysis has shown a pattern where the body size of the grey seals in the Stora Förvar cave changes with time; they become increasingly younger and smaller (Apel & Storå 2018:294p). It has been suggested that this size variation shows that hunting took place during different seasons, as sub-adults are hunted at other times of year (Apel & Storå 2018:294p). Over-harvesting of pups could have affected the future population, i.e. if too many young seals were killed before they reached sexual maturity. Large mammals are sensitive to juvenile mortality, since this determines recruitment (Gaillard 1998).

In our study we also carried out genetic sex identification to study the sex ratio in the hunted seals, and to detect any indication of a preference for one sex over the other. Among the Mesolithic grey seals on Stora Förvar we found 22 males and 29 females, which is an almost equal sex ratio. Thus, there was no clear pattern of selective hunting in this sense. The low genetic diversity among the earliest seals in Stora Förvar could also indicate a high susceptibility to different diseases, e.g. the phocine distemper virus that we know were the subject of devastating outbreaks among phocines in northern Europe in 1988 and 2002. If virus-infected seals migrated into the Baltic Sea, to an isolated and immunologically naïve grey seal population, it could have affected the population negatively.

Comparing the Bronze Age/Iron Age samples from Stora Förvar, dated to between 1,123–883 cal BC and cal AD 675–844, with the historic and modern dataset, we found that they are not genetically differentiated. This is likely to be the result of a recolonisation event, and shows that there has been continuity in the grey seal population from as early as the Bronze Age until the present time. This result is concordant with the result in Fietz et al. (2016), which states that the present Baltic grey seal population separated from the North Sea population around 4,200 years ago.

### 5.2.2 Moose

With a weight of up to 500 kg for females and 600 kg for males, the moose (Fig. 11) is the largest living species in the deer family (Franzmann 1981). Its current distribution is circumpolar, from Eurasia to North America, and it primarily dwells in boreal forests (Franzmann 1981).

The moose is a generalist herbivore which feeds on a large number of different plants, and this diet changes with the seasons and localities (Franzmann

1981; Shipley et al. 1998). Besides humans, the wolf and the brown bear (*Ursus arctos*) are some of the few predators that prey on moose (Franzmann 1981). The breeding season for moose is from September to October, and one or two calves are born in May to June the following year (Franzmann 1981; Saether & Haagenrud 1983). The moose cow is already able to reproduce as a yearling, and continues to reproduce up to 18 years of age (Franzmann 1981).

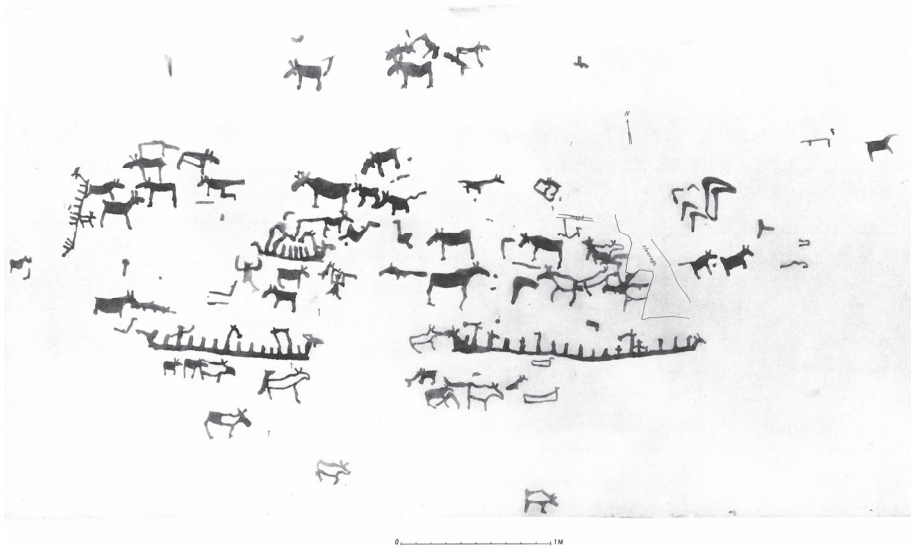


Figure 11. A resting moose cow (I. Przykuta / CC BY-SA (<http://creativecommons.org/licenses/by-sa/3.0/>)).

The moose is a popular game species throughout its distribution range, and this also seems to have been the case during the Neolithic period in northern Sweden. Remains from this period can still be seen at rock-art sites such as Norrfors, Nämforsen and Glösa, where numerous moose are portrayed (Ramqvist 1992:32p). The fact that the moose was popular game can also be seen from the zooarchaeological material from sites which are contemporary with the rock art, e.g. the semi-subterranean structures with surrounding embankments (Larsson et al. 2012). The moose, however, disappears from the archaeological record in northern Sweden around 2,000 cal BC (Larsson et al. 2010), and coincides with considerable societal change in northern Sweden in terms of both subsistence and material culture (Baudou 1977:144p). A similar phenomenon, where the moose disappears from the zooarchaeological material, is also observed in Norway and Finland (Ukkonen 1993; Rosvold et al. 2009). This disappearance also coincides fairly well with the 4.2k event that

caused a shift to a cooler climate with increased precipitation in northern Europe. The 4.2k event has been connected to the disappearance of moose in northern Sweden (Larsson et al. 2012).

In **Paper III** we genetically analysed zooarchaeological bone remains of moose from three Neolithic sites from northern Sweden, with two main aims. The first was to investigate whether the moose hunt was targeting a special part of the population, viz. females. The idea that the hunters selected certain parts of the population derives from the fact that a majority of the moose illustrated on rock art and on other objects do not carry antlers (Fig. 12). This could either be seen as an indication that the hunt took place during the winter when the moose shed their antlers, or that the depicted moose are females or calves which do not carry antlers (Baudou 1977:78pp; Ramqvist 1992:44p; Lundberg 1997:153; Blehr 2014).



*Figure 12. Rock art depiction of moose from Lillforshällan in Nämforsen in Northern Sweden. From (Hallström 1960).*

The second aim was to study which genetic clade the ancient moose population derived from. Previous genetic studies on modern moose have sorted the global moose population into distinct haplogroups: Asian-America (AA), central Europe (C), western Europe (W), and eastern Europe (E) (Niedziałkowska et al. 2014; Kangas et al. 2015; Niedziałkowska 2017; Świsłocka et al. 2020; Dussex et al. 2020). The modern moose population in Sweden is entirely from the western European clade, and is believed to have entered Sweden from the south (Niedziałkowska et al. 2014; Wennerström 2016). Since the moose disappeared from the zoological material, we wanted

to see whether the ancient moose samples from before the Neolithic disappearance originated from the same haplogroup as the present moose population in Scandinavia.

We analysed a total of 32 moose teeth from three Neolithic pithouse sites in northern Sweden: Bastuloken in Ramsele parish (n=10), Agnsjön 1140 in Anundsjö parish (n=8), and Tåsjö 101 in Tåsjö parish (n=14). Sex identification was successful for all samples from Bastuloken, where eight out of 10 sampled individuals were females, which is a significant difference in frequency from males. The samples from Anundsjö and Tåsjö were unfortunately too poorly preserved to extract enough endogenous DNA for continued analysis. Poor preservation of bones from northern Sweden is unfortunately not uncommon, so this result was expected.

Our result indicates that the females were the chosen prey on Bastuloken during this period. Preference for hunting female ungulate cows, as well as female wild boar, has been observed in both North America and Germany (Kay 1994, 1997; Schmölcke 2019). In the German case, the author interprets the result as being linked to the distinct difference in behaviour between males and females (Schmölcke 2019). This could also be the explanation for the overrepresentation of female moose at the Bastuloken site. The moose populations in northern Sweden are partially migratory; some individuals choose to migrate between a summer and a winter pasture, whereas others do not (Singh et al. 2012). Both male and female moose undertake these trips, but the moose cows begin their migration earlier in the year than the males, probably in order to increase the chances of the calves surviving (Singh et al. 2012). This could mean that the females were more susceptible to the hunting activities of people in this area. Whatever the reason for the difference in preferences, a hunting strategy where the females were killed disproportionately could have had a major local impact on the growth of the population (Milner et al. 2007; Doak et al. 2016). The reason for this is the difference in reproductive value, where very young and old individuals have less reproductive value than prime-age individuals, and males have a lower reproductive value than females (see chapter 2.1.1).

The decision to sample teeth could have affected the result. Although cranial bone elements were not underrepresented in the zooarchaeological material from Bastuloken (Storå et al. 2011), the deposition practices may have differed for male and female moose skulls. The male moose skulls may have been used for some special purpose, such as being placed in the bow or stern of boats and on poles as shown on rock art (Zvelebil 2008; Fig. 12), and would hence not be found at the site. A male moose cranial fragment filled with red ochre was found at the Bastuloken site (Storå et al. 2011), which could also be an indication that the male moose crania were treated differently from the female moose crania. For future DNA studies on moose, I therefore suggest analysing a bone element other than teeth.

The second aim of this paper was to compare the ancient moose populations with modern moose populations from other parts of Europe, to see if the temporal genetic structure of moose in Sweden had changed since the Neolithic period. We managed to extract seven mitochondrial moose sequences from the Bastuloken site, which were trimmed to 464 bp to allow them to be compared to reference sequences which had already been published. The estimates of genetic differentiation show that the ancient Bastuloken moose did not differ significantly to modern Swedish and Norwegian moose populations, but they differ significantly from the western European moose clade. All ancient moose from Bastuloken did however fall within the western moose clade (Fig 13). Hence, this result does not support the hypothesis that moose in northern Sweden became extinct at the end of the Neolithic period, when moose disappear from the zooarchaeological material. We can not, however, rule out that an extinction event occurred during the Neolithic period, with later recolonisation of moose with similar haplotypes.

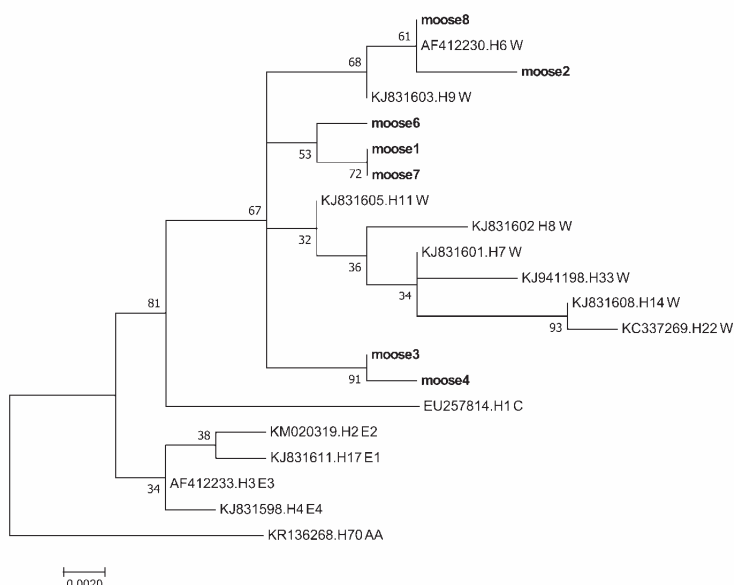


Figure 13. Maximum Likelihood phylogeny of the seven D-loop samples from Bastuloken together with a selected set of reference data.

### 5.2.3 Harp seal

The harp seal (Fig.14) is a subarctic species with a current distribution in the Arctic Ocean and the northern Atlantic, ranging from eastern Canada to northern Russia. Main pupping sites are located in the White Sea and on the east and west coasts of Greenland (Lavigne 2018:455p). There is currently no harp seal population in the Baltic Sea, but skeletal remains from archaeological



sites show that it was a common species in the Baltic from the late Mesolithic onwards (Lepiksaar 1986).

Harp seals differ from grey seals both in terms of behaviour and characteristics. Harp seals are smaller than grey seals, with an adult weight of about 130 kg, and the females are somewhat smaller than the males (Lavigne 2018:455). It is a migratory species which travels long distances and spends considerable time in the sea (Lavigne 2018:456). Harp seals generally give birth to one pup/year, and the weight of the pup at birth is c. 11 kg, though it quickly gains weight during the 12-day lactation period. The lactation period is followed by a 6-week post-weaning period, during which they moult, learn to swim and feed (Lavigne 2018:456). Harp seals are not top predators, and are preyed upon by e.g. polar bears (*Ursus maritimus*), killer whales (*Orcinus orca*) and different sharks (Lavigne 2018:456). Harp seals feed on a large variety of fish like Arctic cod (*Boreogadus saida*), capelin (*Mallotus villosus*), Greenland halibut (*Reinhardtius hippoglossoides*) and invertebrate species (Lawson et al. 1998).



Figure 14. Harp seal on the beach. (Cephas / CC BY (<https://creativecommons.org/licenses/by/2.0>)).

There has been some discussion regarding the occurrence of harp seals in the Baltic, and three hypotheses attempt to explain its presence. One theory is that it was a relict population from the Yoldia Sea stage (Ekman 1922:439pp). Another suggests that harp seals were only present in the Baltic during occasional migrations (Lepiksaar 1986). The third theory is that a breeding population existed in the Baltic, e.g. Lindqvist & Possnert (1997:42). There is now



clear evidence of a breeding harp seal population in the Baltic Sea (Storå & Ericson 2004; Storå & Løugas 2005). The oldest breeding ground was located in the south-western Baltic Sea, and is assumed to have existed not far from the Neustadt archaeological site, dated to between 4,400 and 3,800 cal BC (Glykou 2014, 2016), but the species was present in the Baltic some time before that (Bennike et al. 2008; Glykou et al. 2021). The archaeological record shows that harp seals were hunted extensively during the late Mesolithic and Neolithic periods, until they seem to disappear at the end of the Neolithic period (Løugas 1997; Storå & Ericson 2004; Storå & Løugas 2005; Glykou et al. 2021). Radiocarbon dates show that harp seals were present in the Baltic in two phases divided by a hiatus, when the species was absent (Glykou et al. 2021). The first phase covered the late Mesolithic and the Neolithic periods, followed by a hiatus of c. 1,000 years, and the second phase covered the Bronze Age to the Iron Age (Glykou et al. 2021). Both the presence and disappearance of the Baltic harp seal population is puzzling, and in **Paper IV** we wished to investigate the following. Firstly, what was the origin of the ancient harp seal populations in the Baltic? Secondly, did the ancient harp seals form genetically unique populations? Thirdly, why did the harp seal disappear from the Baltic?

In an attempt to answer these questions, we analysed the mitochondrial genomes from 49 ancient harp seals from the Baltic Sea, the White Sea and west Greenland, dating from the late Mesolithic period to the Iron Age, and compared these to modern harp seal populations in Newfoundland, the Greenlandic Sea and the White Sea (Carr et al. 2015). We found some new haplotypes among the ancient harp seal samples, but they belong to the same haplogroups as those which exist today (see Fig. 15). In other words, the ancient harp seal population in the Baltic basin does not belong to a genetically unique population. The modern harp seal haplogroups are found among most modern harp seal populations, which is expected since the harp seal is a highly mobile species, but there are differences at a sub-haplogroup level. The results of the Kst and Kst\* analyses show that the genetic differentiation is significant between the ancient Baltic Sea and the modern populations.

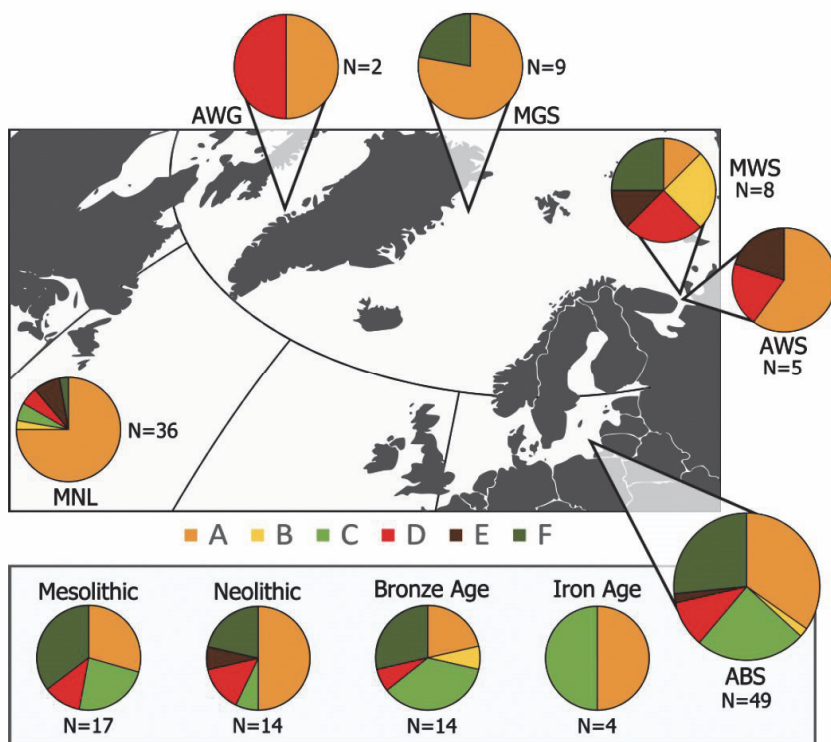


Figure 15. Presence of diverse haplogroups at different sites and time periods. Modern Newfoundland (MNL), ancient west Greenland (AWG), modern Greenlandic Sea (MGS), modern White Sea (MWS), ancient White Sea (AWS), ancient Baltic Sea (ABS). The haplogroups are colour-coded: orange (A), yellow (B), light green (C), red (D), brown (E) and dark green (F).

A comparison between the ancient samples in the Baltic show that nucleotide diversity was at its highest during the Mesolithic period, and gradually decreased through the Neolithic, Bronze Age and Iron Age (Fig. 16). Nucleotide diversity during these time periods is higher than in modern harp seal populations, which shows that the modern harp seal population has undergone a bottleneck at some point in time. There was a gradual decrease not only in nucleotide diversity in terms of Baltic harp seals, but also in their body size. This decrease in adult body size is observed from the late Mesolithic to the hiatus (Storå & Ericson 2004; Glykou et al. 2021). This has been attributed to the genetic isolation of harp seals in the Baltic basin (Storå & Ericson 2004). Interestingly, after the hiatus the harp seals does not show decreased body size as it does in preceding periods. The reason the harp seal disappears at the end of the Neolithic period is not easily elucidated, though overexploitation, inter-

specific competition, genetic drift and climatic fluctuations have been suggested as contributing factors (Storå 2001; Storå & Ericson 2004; Bennike et al. 2008; Glykou et al. 2021).

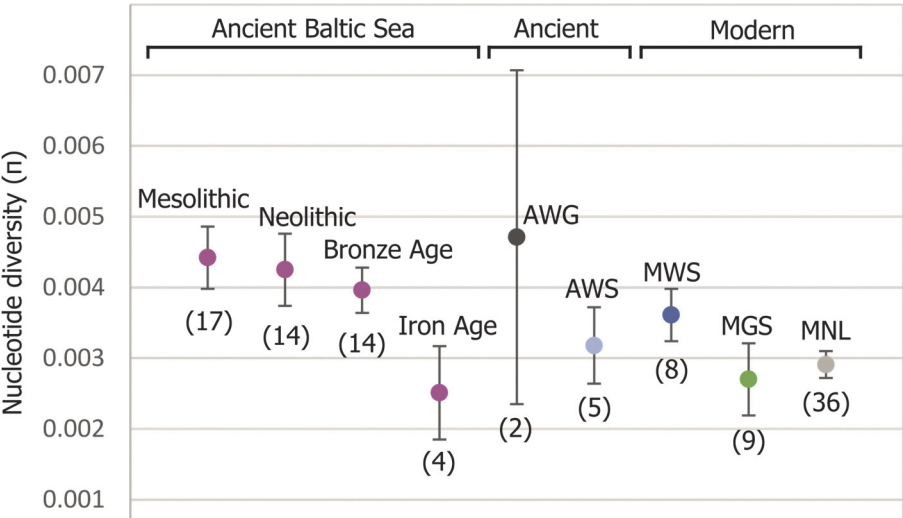


Figure 16. Nucleotide diversity for Baltic harp seals is at its highest during the Mesolithic and Neolithic periods, but gradually declines. The numbers in brackets represent the number of samples. Standard variation (SD) is shown by the error bars. Ancient west Greenland (AWG), Ancient White Sea (AWS), modern White Sea (MWS), modern Greenlandic Sea (MGS) and modern Newfoundland (MNL).

There are no radical changes in the number of haplogroups between the Neolithic and Bronze Age samples according to figure 15, which is especially interesting since the hiatus, when the harp seal is missing from zooarchaeological contexts in the Baltic basin, occurs between these periods (Forstén & Alhonen 1975; Glykou et al. 2021). Our Skyline Plot analysis assumes a continuous population of harp seals throughout the investigated time period and shows a substantial amount of new genetic variation among harp seals in the Baltic Sea in connection to the hiatus. A decrease in the number of haplogroups could be expected when the harp seal disappeared and later recolonised the Baltic Sea after the hiatus, but this does not seem to be the case. This colonisation can probably be explained by a specific aspect of harp seal behaviour, where large groups of individuals from the White Sea occasionally migrate along the Norwegian coast looking for food (Huag & Nilssen 1995; Nilssen et al. 1998; Bennike et al. 2008). In fact, harp seals have been spotted as far south as the west coast of Sweden (Lepiksaar 1986). Large numbers of harp seals could therefore have entered the Baltic Sea during a recolonisation

period, which would explain the large number of haplogroups. The nucleotide diversity is, however, lower after the hiatus than it was before this event.

There is also a possibility that the harp seals were not entirely absent from the Baltic Sea between the Neolithic and the Bronze Age, but that the population underwent a decline, and eventually became replaced by the new incoming harp seals. It has previously been suggested that the ancient Baltic harp seals derived from the White Sea (Glykou et al. 2021), and this was supported by the Kst and Kst\* analyses. The Mesolithic harp seal population in the Baltic showed the highest degree of genetic similarity with modern harp seals from the White Sea, which shows that this was either the source population for the Baltic harp seals or that they originated from the same source population. That the harp seals in the Baltic basin derived from the White Sea population is in line with what has previously been suggested (Storå & Lõugas 2005). This genetic similarity is also seen between the White Sea and the Bronze Age harp seals in the Baltic Sea, which is after the hiatus. This suggests that both colonization events, the initial colonization of the Baltic Sea and the recolonization after the hiatus, most likely originated from the White Sea, or alternatively from another ancient population, which is closely related to the modern White Sea population.

## 6. Concluding remarks

Ancient DNA is a powerful tool for studying the demography and biogeography of past animal populations. The DNA result does not, however, stand on its own, and an understanding of both the archaeological and ecological context is essential to be able to draw conclusions from the results. In this study, aDNA was used as a method of investigating extinctions, recolonisation, translocation, genetic bottlenecks and selective hunting of wild mammalian populations. This thesis focused on three main research questions, and attempted to shed light on new aspects by combining aDNA, ecology and archaeology.

- *The first research question aimed to explore whether it is possible to detect extinctions of wild mammalian populations using aDNA analyses, and to distinguish between overexploitation and climatological factors as the cause.*

This study showed that local extirpations can be detected by applying aDNA analysis, as in the case of mountain hares, and grey seals. As shown in (Fig. 17), however, the disappearance is often connected with climatic events as well as periods of cultural change. In **Paper I**, the Mesolithic mountain hare population on Gotland was genetically unrelated to later populations. This suggested that a local extirpation took place which was later followed by the re-introduction of the same species to the island. The reason for the disappearance of the hare on Gotland is ambiguous. Possible causes include the appearance of the red fox on the island, habitat loss in relation to the Littorina transgressions and the cold period that followed the 8.2k event. Another reason, not yet explored, involves the fact that inbreeding could also have contributed to their extinction.

The grey seals on Stora Karlsö, discussed in **Paper II**, disappeared between 6,942 and 6,625 cal BC after a period of extensive hunting. The Mesolithic grey seals are genetically different from the later population, so their disappearance from the area seems to be linked to an extirpation event. The grey seals disappeared from Stora Karlsö in connection with the Littorina transgressions, which could have caused habitat loss and a change in primary production in the Baltic basin, for example. The disappearance of the grey seal was not connected to the 8.2k event or the hiatus in the cave sequence that followed, since it had disappeared several centuries before. Thus, while there

seems to be no connection between the 8.2k event and the disappearance of grey seals from Stora Förvar, other environmental events cannot be totally excluded as factors contributing to the disappearance of grey seals from the site. Since the grey seal females have strong site fidelity, extirpation is a likely cause of their disappearance, but we cannot rule out the possibility that a combination of hunting and climatic events led to the final disappearance.

Moose in northern Sweden, discussed in **Paper III**, were the preferred prey for human hunters throughout the Neolithic period, until they disappeared from the human sphere in both a cultural context and as a food resource. The disappearance of the moose also coincides with the 4.2k climatic event, and it has been hypothesised that this caused the moose population to crash. The genetic data on moose from the Bastuloken site, prior to the disappearance of the moose, show no significant difference between the Neolithic moose and modern moose populations in Sweden. This genetic continuity could indicate that the moose population did not become extinct at the end of the Neolithic, even though it disappears from the archaeological source material. It could be that the moose became rare, forcing people to switch to different prey.

**Paper IV** discussed the history of the harp seal in the Baltic Sea. The harp seal disappears from the archaeological record in the Baltic Sea from c. 2500 to c. 1545 cal BC (Forstén & Alhonen 1975; Glykou et al. 2021). This disappearance is not, however, obvious in the genetic data, although a slight decrease in nucleotide diversity can be observed between the Neolithic Baltic Sea harp seal population before the hiatus, and the Bronze Age population living in the Baltic Sea after this event. There are as many harp seal haplogroups before the hiatus as after it. Instead, an increase in body size can be observed in Bronze Age harp seals, as well as the introduction of a new haplogroup. This indicates that the Baltic Sea was recolonised by a new group of harp seals sometime during the Bronze Age, and that this was linked to the migratory events undertaken by harp seals, where large numbers of seals travel along the Atlantic coast in search of food. This extinction event would not have been easily observed using only aDNA, which show the importance of the archaeological data.

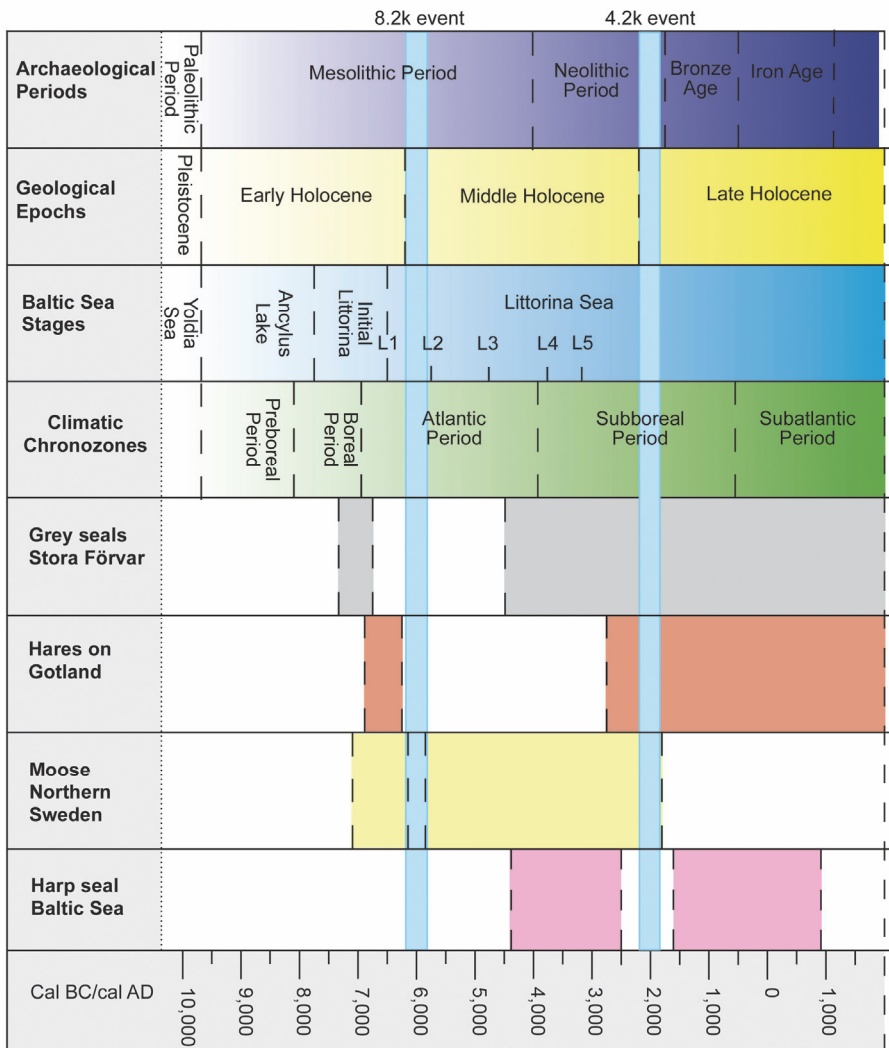


Figure 17. The figure shows the connection between archaeological periods, Baltic Sea stages and climatic chronozones in terms of the presence and absence of the species mentioned in the case studies. From Mangerud et al. 1974; Berglund et al. 2005; Ekholm 2021; Glykou et al. 2021 and Nationalencyklopedin, accessed 2021-09-12

- Another key research question was to investigate whether it is possible to detect human-mediated transportation of wild mammals in prehistory and to distinguish this from natural dispersals.

As described in chapter 2.1.2, human-mediated transportation can be detected if certain criteria are met. An island like Gotland, which was covered in ice during the last glacial period and which has never since been connected to the

mainland, meets these prerequisites. Furthermore, the distance to the mainland makes it hard for most mammalian species to reach Gotland on their own, as shown by the lack of terrestrial mammals in the island's prehistory. Different mammalian species also have traits which make them less likely to embark on long-distance dispersals. In the case of the mountain hare in **Paper I**, the females have strong site fidelity, making the trip from the mainland to Gotland less likely. The aDNA analyses also showed that two different populations of hares came to Gotland on two separate occasions. During the Mesolithic, they were brought to the island during a period when Gotland was completely devoid of terrestrial mammals, so the motivation to introduce a species should have been strong. Studying the history of hares more closely also reveals that they are one of the most translocated mammalian species at global level, both in prehistory and in historic times. This all makes human-mediated transportation the most likely explanation for the appearance of the mountain hare on Gotland.

- *The final research question addressed in this thesis involved detecting whether targeted hunting was carried out on wild mammalian populations in Scandinavia during the Stone Age*

In terms of grey seals, previous studies have already concluded that hunting targeted the young. In **Paper II**, we analysed whether grey seals were targeted according to sex by the human hunters. This is an important aspect to investigate, since it could affect the chances of survival of the population, especially if the hunt was biased towards females. It does not seem that there was any targeted hunting on the basis of sex during the Mesolithic grey seal hunt on Stora Karlsö, as the sex ratio among the seals was evenly distributed. Nevertheless, the grey seal population did disappear after a period of intensive hunting. Although the sex ratio among the prey was equal, it could be that the pups were killed in a way which halted the regeneration of the population.

For moose in **Paper III**, the results show that eight out of the ten individuals analysed were females, so this would suggest that the hunt targeted females, at least at this Neolithic site. This result was particularly interesting considering the presence of moose without antlers on rock art in the interior of northern Sweden during this period. This could suggest that female moose were preferred by the hunters, but it could also be due to different behaviour between males and females which would make the females more vulnerable to hunting. The sample size for this study is small, so the result could possibly be explained by sampling bias. Equally, the study was based on teeth, and it could be that the skulls from male moose were treated differently to the skulls from female moose, and placed in the bow or stern of boats as visualised on rock art, for example (Fig 12). To solve this, future studies should be aimed at different bone elements.



This thesis has shown the importance of studying the genetic history of mammalian populations, and of combining the resulting information with the specific physiology and behaviour of a species, as well as with environmental events and human culture which may have had an impact on these animal populations. Combining all this information provides a clearer picture of the history of the species. It can detect events such as extinctions, and provide insights into the different factors which may have affected animal as well as human populations in prehistory.

## 7. Sammanfattning

Det är lätt att tänka sig att människans först nyligen började påverka sin livsmiljö. Det stämmer att denna påverkan ökade kraftigt i samband med industrialiseringen i slutet på 1800-talet, men samma tendenser går att spåra långt bakåt i tiden. Denna avhandling syftar till att belysa den påverkan som människor har haft på djur i förhistorien, närmare bestämt hur grupper av jägarsamlare påverkade vilda djurpopulationer. Med hjälp av analys av gammalt DNA, och till viss del stabila isotoper samt  $^{14}\text{C}$ -dateringar av animaliskt skellettmaterial från ett antal arkeologiska platser har det varit möjligt att studera demografiska förändringar hos dessa djurpopulationer. Dessa förändringar diskuteras därefter mot information om klimatförändringar, jakt och förflyttningar av vilda djur.

I kapitel 1 beskrivs avhandlingens syfte samt frågeställningar. Här sammanfattas också tidigare forskning i ämnet människans påverkan på djurpopulationer som är ett forskningsfält som studeras av flera olika discipliner. Då denna avhandling är tvärvetenskaplig diskuteras också den tvärvetenskapliga arbetsprocessen.

I kapitel 2 beskrivs olika avseenden där människan påverkar vilda djur. En distinktion görs mellan direkt och indirekt påverkan på däggdjur. Den direkta påverkan är direkt riktade mot djuren, tex vid jakt och förflyttningar av djur till nya platser. Även domesticering av vilda djur, som kan anses som en direkt påverkan, redogörs för i detta kapitel. Trots att ingen av delstudierna berör domesticering är det en så väsentlig påverkan på djur att det måste avhandlas. Indirekt påverkan är när människors handlingar påverkar djur trots att det inte är det huvudsakliga syftet. Exempel på indirekt påverkan är då människans förändringar av sin livsmiljö även påverkar de djur som lever i denna miljö. Röjning av skog och mark för att göra plats för jordbruk är exempel på hur människan påverkar sin livsmiljö. De olika distinktionerna direkt och indirekt påverkan är förenklade begrepp som i själva verket är sammanvävda i varandra. Förflyttningar av djur till nya platser som beskrivs som en direkt påverkan på djurpopulationer skapar också en indirekt påverkan på miljön dit djuren flyttas, samt de djurarter som lever där. Sammanfattningsvis går det att säga att människors direkta och indirekta påverkan av sin miljö inte behöver vara något negativt. Det som är en nackdel för en art kan vara en fördel för en annan. I detta kapitel redogörs också för förändringar av miljön där människan

inte är drivande, tex vid naturliga klimatförändringar eller händelser som vulkanutbrott, tsunamis eller spridning av sjukdomar.

Kapitel 3 utgörs av en beskrivning av tidsperioder i de geografiska områdena som avhandlingen behandlar. Här beskrivs hur djur och människor koloniserade den skandinaviska halvön när istiden var över samt hur de levde under kommande årtusenden. Kapitlet beskriver Skandinavien under stenåldern, men då informationen här ämnar knyta an till avhandlingens delstudier är det ingen komplett redogörelse av tidsperioderna utan snarare ett komplement till artiklarna. För norra Sverige ligger fokus på Neolitikum medan Mesolitikum prioriteras för de södra delarna av Sverige.

Kapitel 4 beskriver de metoder samt material som har använts i studien. Fokus ligger på gammalt DNA; fältets historia, vilka användningsområden som finns, samt vad det finns för svårigheter med metoden. I detta kapitel beskrivs Stora Förvar och Bastuloken något mer utförligt då de får anses vara avhandlingens viktigaste arkeologiska platser, medan övriga arkeologiska platser bara benämns i en lista.

Kapitel 5 är ett diskussionskapitel där resultaten från de olika delstudierna diskuteras i relation till frågeställningarna. Här ges också bakgrundsinformation om de olika djurarterna.

I kapitel 6 ges en sammanfattning av resultaten i de olika delstudierna i relation till avhandlingens frågeställningar.

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