Jørgen Rosvold

Ungulates in a dynamic and increasingly human dominated landscape

A millennia-scale perspective

Thesis for the degree of Philosophiae Doctor

Trondheim, January 2013

Norwegian University of Science and Technology
Faculty of Natural Sciences and Technology
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Preface

"*Jack of all trades, master of none?*"

Species can generally be categorised into two groups: specialists or generalists. While a specialist focus on one area, and becomes particularly good at that, a generalist make use of a wide range of resources. I guess the same can be said about researchers and research projects. This work is certainly of the latter category, combining ecology with elements of archaeology, anthropology, chemistry, genetics, osteology and physiology. I must admit that I was a bit worried at first by the range of different disciplines that I had to familiarise with, exceeding my training as an ecologist. I am no expert on any of these fields, but these four years of my PhD has thought me a lot and given me a new look on nature that I would not be without. This generalist approach means that you only get a peek into each of the different subjects, but together they tell a different and highly interesting story than what would have been possible by delving extensively into one area. However, this approach also meant that I had to rely on the expertise of others and this project would not have been possible without the aid of a range of great people.

I am deeply grateful to my supervisors Reidar Andersen and Hans K. Stenøien, and co-supervisors Anne Karin Hufthammer and Knut H. Røed who guided me through the process. Reidar Andersen started out as my main supervisor and has been a good mentor for more than seven years. His enthusiasm and grand visions have been a huge motivating force, and he always manages to switch on my optimistic side. Halfway through my PhD Reidar got the job as director of SNO and had to step down as my main supervisor, but he has nonetheless been involved in the project with as much interest and support throughout. Hans K. Stenøien took over as my main supervisor in 2011. His expertise in genetics and keen eye for details has greatly improved my work, and I am very grateful for his efforts during the final stages of my PhD. Anne Karin Hufthammer at Bergen Museum has kindly opened her vault to the great mass of ancient bones waiting to be analysed, has shared of her deep osteological knowledge and thought me the value of such a material. Last but not least I am thankful to Knut H. Røed at NVH who took a clueless ecologist into his lab and thought him genetics. The many months spent at his lab were a pleasure.

I also thank my co-authors for their great collaboration. Thanks to Duncan J. Halley for teaching me about the world of stable isotopes and to Masao Minagawa for making his facilities available for our use. I'm grateful to John D.C. Linnell for his valuable input on ecology and wild ungulates, and to Ivar Herfindal for helping me interpret my morphological measurements with his statistical and ecological expertise.

Many others have also been involved in the project at different stages. I would especially like to thank Liv Midthjell and Gro Bjørnstad at NVH for teaching me their laboratory procedures and for putting up with my difficult questions, and to Ellen

Gunby and all the people at the genetics lab for making my stay a pleasure. Thanks to Tore Fredriksen and Olaug Bratbak for aid in sorting through bone samples and to Hallvard Haanes for valuable discussions on the genetics of red deer. I am very grateful to Ola Magnell for information on Swedish material and, although we got no results, for great aid in providing Swedish samples for DNA analysis. Thanks to Johan T. Solheim for lending me good photos of red deer and for help with getting hold of female red deer skeletons, and to Frode Holmstrøm for helping me clean out the bones. I am grateful to Per Gätzschmann for aid in prying out very stubborn molars from their jaws. I would also like to thank Heidi M. Breivik for valuable archaeological discussions and comments, and Arne B. Johansen for tuning my mind to long-term thinking. Thanks to all the archaeologists who have provided me with additional information regarding their excavations. I am also grateful to the staff at the Gunnerus Library for satisfying an endless demand of obscure papers and books.

This thesis was funded by and carried out at NTNU Museum of Natural History and Archaeology, and the Department of Biology. I have had the pleasure of spending time and working with people from all of the different sections of the museum and great thanks goes to all for making my stay here a pleasure and making me feel like part of the team. Special thanks go to Per Gustav Thingstad for sharing his knowledge about birds and mammals, and for giving me highly interesting and varied duties besides my PhD. This has included field work, management, museum collections, exhibitions and communications with the public and media.

I am very thankful to the Directorate for Nature Management who provided funds for the project. Hopefully you will feel that this was money well spent.

Thanks to all of my family and friends for putting up with my busy schedule. I hope you still remember who I am even though I have spent the last months locked up at my office and secluded from the outside world.

Very special thanks go to Astrid B. Lorentzen for sticking with me for the last ten years. Her knowledge in archaeology and GIS has been a great help as well as our discussions on both nature and culture. Both her continued support and critical evaluations have been invaluable. Thanks for calming my stress levels and reminding me that there are even more interesting things in the world than dry old bones. This one is for you.

Trondheim, July 2012

Jørgen Rosvold

CONTENTS

LIST OF PAPERS

The thesis is based on the following four papers:

I) Rosvold J, Halley DJ, Hufthammer AK, Minagawa M & Andersen, R (2010): The rise and fall of wild boar in a northern environment: evidence from stable isotopes and subfossil finds. *The Holocene* 20 (7): 1113-1121.

II) Rosvold J, Andersen R, Linnell JDC & Hufthammer AK (manuscript): Cervids in a dynamic landscape: Holocene changes in moose and red deer abundance along the limit of their distribution.

III) Rosvold J, Røed KH, Hufthammer AK, Andersen R & Stenøien HK (submitted): Reconstructing the history of a fragmented and heavily exploited red deer population using ancient and contemporary DNA.

IV) Rosvold J, Herfindal I, Andersen R & Hufthammer AK (manuscript): Long-term morphological changes in the skeleton of red deer at their northern periphery.

Declaration of contributions

I) JR, AKH and RA initiated and designed the study. JR and AKH gathered data on the sites and picked out the samples. DJH performed the stable isotope analysis using the laboratory of MM. JR reviewed the sites and historical documents, and wrote the manuscript with contributions from all co-authors.

II) JR did the laboratory work, analysed the data and drafted the manuscript. HKS performed the ABC-analyses. JR and AKH picked out the ancient samples. KHR supervised the laboratory work. All authors were involved in the study design, revising of the manuscript and read and approved the final manuscript.

III) All authors were involved in the conception and design of the study. JR and AKH gathered data on the sites and picked out the samples. JR analysed the data and wrote the manuscript with contributions from all co-authors.

IV) JR, RA and AKH initiated the project. JR and AKH designed the study. JR performed all the measurements, analysed the data and drafted the manuscript. IH performed some of the statistical analyses. All authors were involved in revising the final manuscript.

INTRODUCTION

> "*Study the past if you would divine the future*"
>
> Confucius

That nature is dynamic and in a constant state of change is a well established fact in ecological theory, but still much ignored in politics, management and conservation practices (Smith *et al.*, 1993; Jelinski, 2005). This dynamism is created and maintained by both external and internal factors, e.g. solar cycles, plate tectonics, climate change, evolution and changing biotic interactions. An understanding of this constantly changing nature is crucial for good management of natural resources, as this is not just an aspect of the past but also of the future.

Due to strong human influence and expected climatic change, the future of the world's biodiversity is generally considered to be under threat (Sala *et al.*, 2000; Steffen *et al.*, 2007; Bellard *et al.*, 2012). Future environmental changes are expected to cause dramatic changes in the distribution, phenology, physiology and genetic diversity of species, and there is a focus on trying to estimate if populations can adapt quickly enough to cope with these rapid changes and how many will go extinct (i.e. Woodruff, 2001; Bradshaw and Holzapfel, 2006; Chevin *et al.*, 2010; Frankham, 2010; Reed *et al.*, 2010; Visser, 2010). Most conclusions are, however, drawn from theoretical models or studies only considering the last decade or so, or in some few cases the last hundred years, often forgetting the fact that large scale and rapid environmental changes are not new phenomena. Knowing how organisms have responded to such dynamics in the past may help us to understand their current responses to environmental changes and potential for future adaptations. History may not repeat itself in exactly the same manner but, as Mark Twain (1835-1910) allegedly said, "… *it does rhyme*".

In its nature, archaeozoology needs to understand periods ranging from centuries to millennia and the data must be interpreted from a great variety of both environmental and anthropogenic factors. This puts archaeozoology in an exceptional position for understanding long term changes in the fauna and may provide time series many times longer than studies of contemporary populations (Frazier, 2007). By giving information on past states or how changes in climate and human exploitation have influenced the fauna it should be a valuable tool for both conservation and management but have so far been sparsely used (Briggs *et al.*, 2006; Lyman, 2006; Willis and Birks, 2006). One of the goals of this thesis is to show the usefulness of archaeozoology as a tool for current management, by exploring relevant issues using archaeological material of economically important species from the Holocene (i.e. the last 11,500 years).

The Quaternary period (i.e. the last c. 2.6 mill years) of repeated glacial and interglacial cycles was a period of huge and often rapid climatic changes with equally large and rapid changes in population sizes and geographic distributions of organisms (Hewitt, 2000; Hofreiter and Stewart, 2009). The Pleistocene epoch of the Quaternary (i.e. until 11.500 years ago) had the most variable climate and has been suggested as a good model for investigating possible effects of rapid climate change (Hofreiter and Stewart, 2009; Pardi and Smith, 2012). However, the Holocene has also seen large climatic fluctuations, including periods with climate similar to projected future warming (e.g. Karlén, 1998; Solomon *et al.*, 2007). This was also the time when agriculture spread across the world, transforming the landscape and allowing the human population to increase dramatically (Fagan, 1999). The Holocene period should thus be a good model for studying the interplay of human activities with climate and its increasing influence upon the environment of other species.

Responding to environmental change

Environmental change is a continual factor in the lives of all organisms and probably no individual is faced with a perfectly stable environment. However, some changes have a larger impact than others. As the environment changes animals are faced with three options: adapt to the changing conditions, move to a new area containing suitable habitat or eventually go extinct. The outcome depends upon a range of environmental factors.

Populations can adapt to environmental changes in two ways: through adaptive phenotypic plasticity or genetic evolution. Although phenotypic plasticity may have a genetic basis and be under selection (Windig *et al.*, 2004) it is defined as the ability of an organism to produce alternative phenotypes in different environments (DeWitt and

Scheiner, 2004), e.g. the ability to change diet in relation to available resources or morphological changes in relation to predator density or temperature. Plastic traits may allow populations to react quickly to the environment without any genetic changes. However, there are costs and limitations associated with plasticity and in the long run evolutionary change may be more cost-effective and able to produce more extreme phenotypes than plastic responses (DeWitt *et al.*, 1998; Chevin *et al.*, 2010). The ability to evolve quickly enough to environmental change is dependent on a range of factors including the direction, strength and speed of the selective environmental change; the plasticity and evolvability of the various traits under selection; demographic parameters like generation time and population growth potential; inter- and intraspecific interactions; gene flow; and of course sufficient genetic diversity (Hansen and Houle, 2008; Johansson, 2008; Chevin *et al.*, 2010; Visser, 2010).

The genetic diversity of a population is generally a good measure of its ability to adapt to future environmental changes and, as loss of genetic diversity is directly related to inbreeding, its current reproductive fitness and extinction risk (Frankham *et al.*, 2002). Mutations are the source of new genetic variation and the genetic diversity of a population is an effect of mutation rate, selection, breeding system, population size and gene flow, but also of historic factors (ibid.). Because of genetic drift (random fluctuations in allele frequencies) small and isolated populations loose genetic diversity faster than large populations (Wright, 1931; Nei *et al.*, 1975; Frankham, 1996). Reductions in population size including loss of genetic variation are termed population bottlenecks (Nei *et al.*, 1975) or a founder event if this is an effect of a small number of individuals establishing a new population, e.g. through post-glacial colonization. Such events in the history of a population has shaped its current genetic diversity and this diversity is a result of the number and magnitude of as well as the time since these events (Frankham *et al.*, 2002; Freeland, 2005). Strong genetic drift and population isolation may also lead to population differentiation, while migration can introduce new genetic variation from other populations (Wright, 1951; Nei *et al.*, 1975; Frankham *et al.*, 2002). Immigration of individuals with different adaptations does, however, also have the potential to replace local adaptations (Rhymer and Simberloff, 1996; Frankham *et al.*, 2002; Fitzpatrick *et al.*, 2010).

If species or populations are unable to adapt to environmental changes they are forced to alter their distributions to track these changes, or if unable to do so their populations will decrease and eventually go extinct. Good examples of such changes in distribution are the Pleistocene cycles of repeated ice ages in Eurasia and North America, pushing species south during cold periods and north during warmer periods (Graham, 1986; Webb and Bartlein, 1992; Hofreiter and Stewart, 2009). The range of a species is a product of habitat selection, climatic tolerance, interactions with other species and dispersal abilities (Darwin, 1859; Krebs, 2001). These factors are interlinked and in response to changing climate differences in dispersal abilities and adaptability may lead to species specific responses and thus to changes in community structure and biotic interactions over time (e.g. Graham and Grimm, 1990; Davis *et al.*, 1998; Van der Putten *et al.*, 2010). At the edge of its range a species is by definition living in a marginal habitat and thus environmental changes are expected to have the most pronounced effects on populations at the range edges (Haldane, 1956; Williams *et al.*, 2003). Populations living in edge areas are often characterized by increased genetic differentiation and more stochastic population dynamics (Sexton *et al.*, 2009), which in turn makes them more prone to extinction (Lande *et al.*, 2003). Studying ecological responses to environmental change at range edges has been claimed as a key for understanding the future of populations (Holt and Keitt, 2005; Sexton *et al.*, 2009).

All species modify their environments; however, few species have such a profound and widespread influence on their community as humans (Vitousek *et al.*, 1997b; Goudie, 2006; Steffen *et al.*, 2007; Ellis and Ramankutty, 2008). Through heavy harvesting, habitat fragmentation, pollution and translocation of plants and animals our activities have the potential to affect most aspects of the lives of other organisms and thus their evolutionary trajectories. Heavy harvesting may cause reduction in the distribution and density of other species and has caused the extinction of some, e.g. the great auk (*Pinguinus impennis*), the passenger pigeon (*Ectopistes migratorius*) and the thylacine (*Thylacinus cynocephalus*) (Halliday, 1980; Bengtson, 1984; Guiler, 1985). In addition, there is evidence that harvest may cause changes in life history characters like body size and age of first reproduction of harvested species (Fenberg and Roy, 2008; Allendorf and Hard, 2009; Darimont *et al.*, 2009; Sharpe and Hendry, 2009). Introduced animals may compete with, prey on or hybridize with native animals (Rhymer and

Simberloff, 1996; Vitousek *et al.*, 1997a; Salo *et al.*, 2007). Landscape alterations, and especially the conversion of forests into agricultural and urban land, cause loss and fragmentation of suitable habitats, may isolate populations and thus prevent migration and habitat tracking (Fahrig, 2003; Travis, 2003).

These large scale anthropogenic influences are largely attributed to events during the last 2-300 years, i.e. after the industrial revolution and the exponential human population growth (Turner II *et al.*, 1990). Prehistoric environmental changes caused by humans are usually seen as negligible in relation to this, leading to the present changes being seen as “unnatural” and creating a need for finding a more “natural” state as a comparison for conservation and management (Hofgaard, 1999; Jackson, 2001; Willis and Birks, 2006; Bischof *et al.*, 2008). However, humans may have had a strong influence upon their communities and habitats for a much longer time, with evolutionary consequences for other species. Humans have hunted and used fire for several hundred thousand years and inhabited most of the world, performed agriculture and transported animals for more than 10,000 years (Fagan, 1999; Grayson, 2001; Roebroeks and Villa, 2011). While this is well known, less is known about how it affected the ecology and evolution of other species and how this is manifested in present day populations.

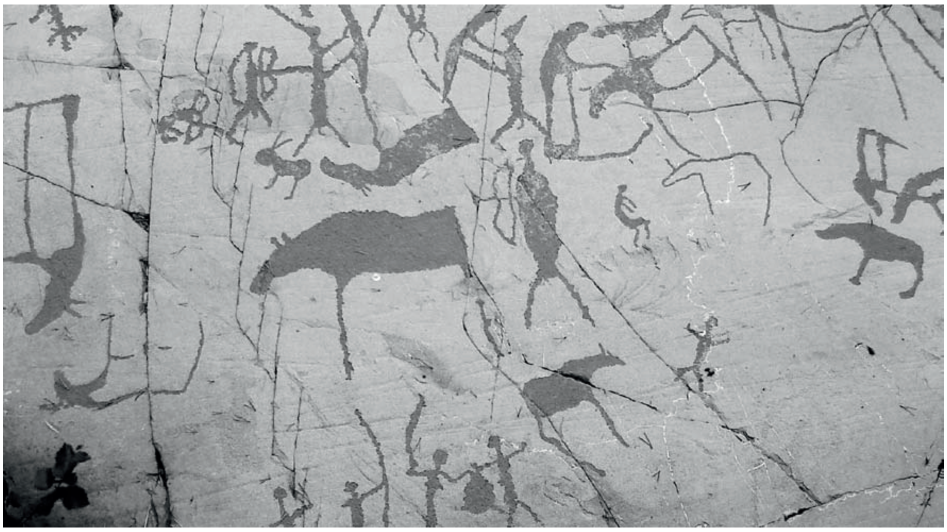


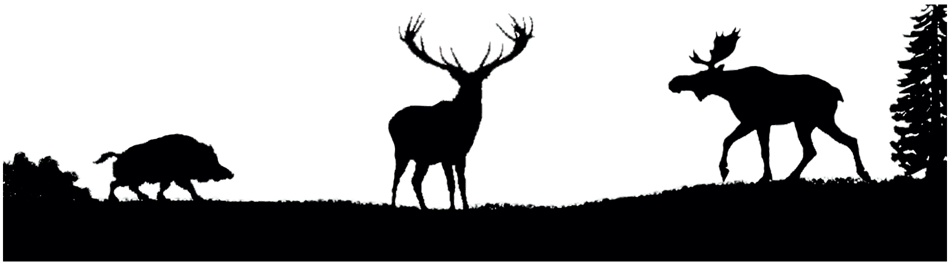
Figure 1: Prehistoric hunting scenes engraved in rock. Photo: © Astrid B. Lorentzen

AIMS

This study was undertaken in order to gain increased insight into the history of moose, red deer and wild boar in Norway. The main aim of the thesis has been to gain a deeper understanding on how climate and human use of natural resources may interact or counteract in their effects upon other species. This is important as major changes in both of these factors are expected within the next century. Profound changes in the environment of species are not a new phenomenon and an understanding of how the fauna has reacted in the past may thus help us to comprehend the consequences of future changes. This thesis addresses this issue by examining several aspects of wild ungulate ecology in an increasingly human dominated landscape, focusing on the transition from a “natural” to a more cultural landscape during the Holocene in lowland western Norway.

More specifically the main aims of the papers were:

1) Can we differentiate prehistoric wild boar from early domestic pigs based on stable isotopes? (paper I)
2) What was the prehistoric habitat of wild boar in Norway and can it shed light on what limits their northward dispersal? (paper I)
3) How was the distribution and abundance of wild ungulates in western Norway related to large scale environmental changes throughout the Holocene? (paper I and II)
4) How was the genetic diversity of red deer affected by long term population fragmentation and heavy harvest during the last millennia? (paper III)
5) Is the contemporary population of red deer in Norway descended from native prehistoric animals or a result of human mediated translocations of foreign deer? (paper III)
6) How has the morphology of red deer changed through time and are the changes related to any of the large scale environmental changes during the Holocene? (paper IV)



STUDY SPECIES

Four species of wild ungulates currently inhabit lowland parts of Norway: red deer (*Cervus elaphus*), moose (*Alces alces*), wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*). Roe deer does, however, seem to have been very rare in Norway up until the last century, as only four subfossil bones in total have been found of the species (Hufthammer, 1992; Hufthammer and Aaris-Sørensen, 1998). This study is therefore limited to red deer, moose and wild boar, which represent the three largest and most important terrestrial lowland game species in prehistoric Norway. These three ungulates would have been considered valuable resources of meat, fat and raw material, and possibly as trophy species. They have been hunted for most of the Holocene and are some of the most common faunal representatives in archaeological bone collections (Hufthammer, 2006). They have different habitat adaptations and we therefore expect different reaction patterns to various environmental changes. Common for all of them is that they were present in Norway for thousands of years after the Last Ice Age, have suffered a dramatic population decline leading to extinction or near extinction, and have experienced a rapid population increase during the recent decades. Red deer has the most continuous distribution of skeletal remains through time and most of the investigations in this thesis are therefore based on red deer.

Figure 2: The study species. Photos: Wild boar and moose; © Jørgen Rosvold. Red deer; © Johan Trygve Solheim, Norsk hjortesenter.

Wild boar

Wild boar are among the most widespread and adaptable species in the world, being found in every continent except Antarctica (Powell, 2004; Wilson and Mittermeier, 2011). They are primarily associated with temperate and tropical forests, but its present range includes parts of Russia with average winter temperatures as low as -20°C (Markov *et al.*, 2005). Wild boar are medium sized ungulates ranging from 35-350 kg in weight and 55-110 cm in shoulder height, with males being larger than females (Powell, 2004; Wilson and Mittermeier, 2011). Reproduction is opportunistic and highly dependent on body weight (Fernández-Llario and Mateos-Quesada, 1998; Gethöffer *et al.*, 2007), with litter sizes normally varying between 5-9 piglets (Wilson and Mittermeier, 2011).

The wild boar has a body construction adapted for finding food primarily on or in the ground. They are typical omnivores, eating a huge range of different plants, animals and fungi, but their diets include at least one high energy food source (Schley and Roper, 2003). In order to get to these foods they may raid agricultural crops (Genov, 1981; Schley and Roper, 2003). Their rooting behaviour means that long periods of heavy snow and frozen ground may increase mortality in young and weak animals (Jedrzejewski *et al.*, 1992; Okarma *et al.*, 1995). Young piglets are particularly sensitive to cold (Berg *et al.*, 2006), but the sows have compensated for this by building isolating farrowing nests (Algers and Jensen, 1990; Danilov and Panchenko, 2012). Females and young animals generally live in large family groups, while the males range over larger distances. At lower densities these groups are more unstable (Spitz, 1992), and dispersal frequencies are inversely related to population density (Janeau and Spitz, 1990; Truvé *et al.*, 2004).

The wild boar is currently not considered a native species in Norway and is cited on the “Norwegian Black List” of alien species (Gederaas *et al.*, 2012). However, the neighbouring Swedish population have increased dramatically during the last decades (Lemel and Truvé, 2008) and animals have started crossing the border into Norway (Haaverstad, 2011). It is thus expected that wild boar will establish themselves in several areas in the near future (Rosvold and Andersen, 2008).

Moose

The moose has a circumpolar distribution tied to the boreal coniferous forests or the mixed forests of the northern temperate zone (Geist, 1998; Wilson and Mittermeier, 2011). It is the largest terrestrial species in Norway, weighing between 280-600 kg and has a shoulder height of 185-210 cm; with bulls being 25-30% larger than cows (Wilson and Mittermeier, 2011). Relative to its size, the moose has a rapid life-cycle with a high reproductive output (Gaillard, 2007). Females normally give birth to up to two calves which grow rapidly during the summer (Geist, 1998).

Moose are very well adapted to life in cold and snowy environments. Their long legs and wide hooves tackle movement in deep snow (Formozov, 1946; Telfer and Kelsall, 1979), and given adequate amounts of food their thick skin and dense fur allow them to withstand temperatures as low as -25°C without any noticeable effect (Renecker and Hudson, 1986). High temperatures seems more critical and increased heart rate and respiration have been observed at temperatures above -2°C in the winter and 14°C in the summer (Renecker and Hudson, 1986). They are primarily selective browsers feeding on deciduous trees like willow (*Salix* spp.), birch (*Betula* spp.) and aspen (*Populus tremula*), as well as pine (*Pinus sylvestris*) during winter, but also grazing on bilberry (*Vaccinium myrtillus*) and other shrubs and forbs (Månsson *et al.*, 2007; Wam and Hjeljord, 2010).

Bull moose are generally solitary for most of the year, while females stay with their calves who often settle close to their mother (Cederlund *et al.*, 1987). They do, however, tend to aggregate into smaller groups during winter, making mutual use their trails through the snow (Geist, 1998). Movement patterns are highly variable but both males and females can migrate large distances between summer and winter ranges (Andersen and Sæther, 1996; Ball *et al.*, 2001). The core areas of Norwegian moose are eastern and central Norway, but they are distributed over most of northern Norway and have increased in numbers towards the west.

Red deer

Formerly recognized as one circumpolar species the red deer and wapiti (*C. e. canadensis* or *Cervus canadensis*) are now increasingly accepted as two distinct species based on genetic differentiation, physiology and behaviour (Geist, 1998; Ludt *et al.*, 2004; Pitra *et al.*, 2004; Wilson and Mittermeier, 2011). Several subspecies of western red deer have been defined, including a distinct Norwegian type (*C. e. atlanticus*), but genetic analyses support only three different subgroups within Europe: western European, eastern European and Mediterranean red deer (Ludt *et al.*, 2004; Skog *et al.*, 2009). These three lineages most likely represent three distinct refugia during the Last Ice Age, i.e. Iberia, Balkan and Sardinia, and most of Europe seems to have been colonized by the western lineage (Skog *et al.*, 2009; Niedzialkowska *et al.*, 2011; Zachos and Hartl, 2011).

The red deer is an adaptable and plastic species, both in morphology and ecology (Lowe and Gardiner, 1974; Geist, 1998; Rivals *et al.*, 2009). It is primarily associated with temperate broadleaf forests and meadows but have adapted well to a range of different habitats (Geist, 1998; Wilson and Mittermeier, 2011). Red deer weighs between 75-350 kg and range in size from about 95-130 cm in shoulder heights, with males being larger than females (Wilson and Mittermeier, 2011). Hinds tend to stay in relatively stable family groups while males may form more loosely structured bachelor bands (Wilson and Mittermeier, 2011).

Red deer are intermediate feeders relying on both grazing and browsing. Their diets are varied but heather (*Calluna vulgaris*), *Vaccinium* spp. and leaves of different deciduous trees and graminoids are particularly important (Ahlén, 1965c; Gebert and Verheyden-Tixier, 2001). In western Norway, the large topographic variation in the landscape allow red deer to track variations in plant growth phenology providing longer access to nutrient rich plants (Mysterud *et al.*, 2001; Pettorelli *et al.*, 2005).

Winter conditions are considered to be the main limiting factor for the northward spread of red deer (Formozov, 1946; Ahlén, 1965c; Mysterud and Sæther, 2011). Compared to the moose, red deer are relatively short legged and not as adapted to movement in deep snow (Formozov, 1946; Ahlén, 1965c). Neither are they as well isolated from cold weather, and energetic costs of thermo-regulation rapidly increase at low temperatures (Simpson *et al.*, 1978; Semiadi *et al.*, 1996). Both males and females perform seasonal migrations between summer and winter areas, but natal dispersal rates are pronouncedly male biased and negatively related to density in males (Loe *et al.*, 2009; Haanes *et al.*, 2011b). The present core areas of Norwegian red deer are the coastal parts of western and central Norway, but they have increased in numbers towards the interior and northern parts of the country during recent decades.

European red deer have a long history of translocations of animals by humans (Linnell and Zachos, 2011), and foreign animals have been imported to the island Otterøya in north-central Norway (Collett, 1909; Haanes *et al.*, 2010b). Apart from that there are no known human-mediated translocations of red deer into the country. However, the relationship of Norwegian red deer with other populations and its native status has long been debated (e.g. Holten, 1800; Stejneger, 1908; Collett, 1909; Ingebrigtsen, 1925; Langvatn, 1998). The reason for this is that Norwegian animals are morphologically dissimilar to the neighbouring Swedish animals with a distinct cranial morphology (Ahlén, 1965b). Allozyme markers also indicate a possibly closer relationship to the Scottish red deer (Gyllensten *et al.*, 1983). Suggested reasons for this dichotomy among the Scandinavian red deer has been long term isolation and subsequent adaptations to different environments (Collett, 1909; Ekman, 1922; Ingebrigtsen, 1925; Ahlén, 1965b), different source populations and colonization routes (Stejneger, 1908; Ahlén, 1965b; Gyllensten *et al.*, 1983), or that the Norwegian population is a result of human mediated translocation of foreign animals (Holten, 1800; Melchior, 1834), possibly by Vikings (Langvatn, 1998; Haanes *et al.*, 2011a). Historic records indicate that the population size of Norwegian red deer was severely reduced in the 17th – 19th centuries AD and at the brink of extinction, being reduced to a handful of small and isolated populations (Collett, 1909).

STUDY AREA

This study considers material from all over Norway, but focus mainly on the southern part and in particular on the lowland areas of western Norway (defined as the counties Rogaland, Hordaland and Sogn & Fjordane; figure 3). This area was chosen as it has a very good record of faunal remains as well as environmental changes during the Holocene, and represents a variety of different climates and vegetation types. Western Norway also has a long and relatively well known history of human occupation, dating back at least 11,500 years (Bang-Andersen, 2012).

Norway is highly diverse in climate, vegetation and topography. From south to north the vegetation changes from nemoral to high alpine and southern arctic vegetation zones (Moen, 1999). Much of the country is mountainous and the Scandes mountain chain creates a natural border of alpine tundra between the climatically distinct western coast and the inland. Coastal areas and the fjords has a distinct oceanic climate with mild winters and cool summers, while the inland and higher lying areas have more pronounced climatic fluctuations with longer and more snow rich winters. Overall precipitation is highest in western Norway but snow cover increases towards the inland and mountains, and may reach considerable depth in certain areas during winter (October-April). Annual temperatures range from about 8°C along the south and west coast to -6°C in mountainous areas, providing western Norway with the longest growing season in the country (ibid.). Broadly speaking eastern Norway is characterized by boreal coniferous forests, the south and west by temperate mixed coniferous and deciduous woodlands and coastal heathlands, and northern Norway by birch forests and alpine vegetation (ibid.).

The western Norwegian landscape is largely broken up by numerous steep and narrow fjords and much of the land is above the tree-line. This coastal high relief landscape contains an abundance of caves and rock shelters which have been utilized by humans and that provide a cool and stable environment for the preservation of skeletal remains.

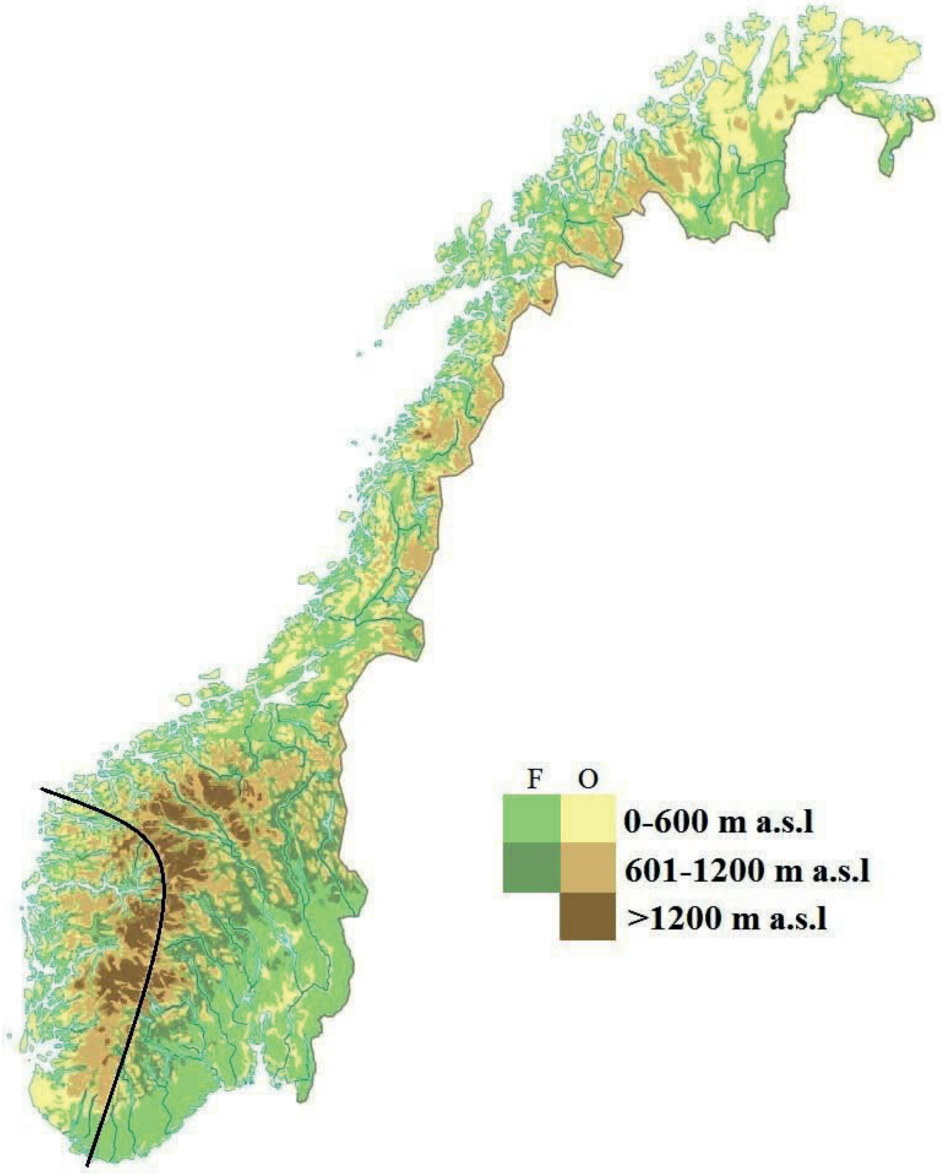
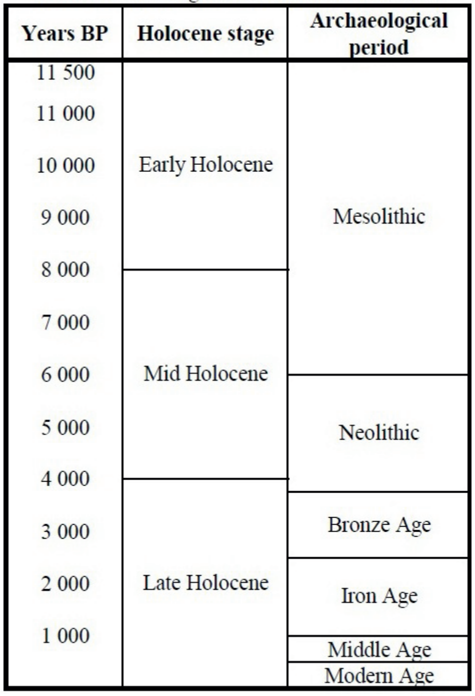


Figure 3: Topographical map of Norway where current forest cover (F) is shown in shades of green and open land (O) in brown shades. Main study area, “western Norway”, is outlined with a black line. Map modified from Kartverket.

TIME PERIOD, CHRONOLOGY AND CONTEXT

The time period considered for this study is the Holocene; the current geological epoch following the end of the Last Ice Age, i.e. the last c. 11,500 years (10,000 ^{14}C years). Unless specifically stated, all dates reported in this study are calibrated into calendar years before present (yr BP). The thesis follow the archaeological chronology of southern Norway given in Østmo and Hedeager (2005) and I have divided the Holocene into three main stages based on climate and human economy (Table 1). The "Early Holocene" represents a pioneer stage for many species, with rising temperatures and rapidly changing vegetation. The "Mid Holocene" represents the Holocene warm period and climax forest vegetation. The "Late Holocene" represents a cooler and drier climate with more open vegetation, increasing human populations and intensive land use. The term "prehistory" refers to the time prior to the Middle Age.

Table 1: Chronological framework for the thesis



Years BP	Holocene stage	Archaeological period
11 500	Early Holocene	Mesolithic
11 000		
10 000		
9 000		
8 000	Mid Holocene	
7 000		
6 000		Neolithic
5 000		
4 000	Late Holocene	
3 000		Bronze Age
2 000		Iron Age
1 000		Middle Age
		Modern Age

The Holocene environmental context

The Holocene was initiated by a rapid and large scale climatic warming, melting the large ice caps that had covered most of the Scandinavian Peninsula during the Last Ice Age (Andersen and Borns, 1997; Mangerud *et al.*, 2011). There is growing evidence of vegetated ice free areas along the coast of Norway (Krüger *et al.*, 2011; Parducci *et al.*, 2012) and around mountain tops (i.e. nunataks) (Paus *et al.*, 2006; Paus *et al.*, 2011) for several millennia before this, possibly allowing the existence of certain terrestrial species like reindeer (*Rangifer tarandus*). However, for most mammals the passage was blocked by ice and sea until a land bridge appeared c. 11,000 – 10,000 yr BP connecting Norway and Sweden to continental Europe in the south (Björck, 1995). Humans, on the other hand, had boats and were able to quickly colonize the ice free areas. The most reliable traces of human occupation show habitation from about 11,500 yr BP and in about 2-300 years they seem to have settled along the entire Norwegian coastline (Bjerck, 1995; Bang-Andersen, 2012). Humans were thus one of the first land mammals to colonize Scandinavia after the Last Ice Age and were present before the main immigration of terrestrial animals.

Temperatures rose rapidly during the Early Holocene and most of the Holocene had summer temperatures warmer than today (Davis *et al.*, 2003). The Mid Holocene was the warmest part, with summer temperatures up to around 2°C higher and winter precipitation up to 225% of today (Bjune *et al.*, 2005). Winter temperatures were also higher and the climate seems to have become more oceanic in the Mid Holocene (Giesecke *et al.*, 2008). Most glaciers were probably completely melted away during this period (Nesje *et al.*, 2008), tree-line altitudes were higher and forest covered much of present day alpine tundra regions (Moe, 1979; Aas and Faarlund, 1988; Bjune, 2005). The Mid Holocene environment were also characterized by dense forests in the lowlands with broad-leaved trees at the southern and western coast (Moe *et al.*, 1996).

Towards the end of the Mid Holocene two major environmental changes began to set in. Climate started getting colder in north-western Europe (Davis *et al.*, 2003) and the Late Holocene in western Norway is characterized as cooler and drier than the previous period (Bjune *et al.*, 2005). Farming and animal husbandry were introduced to Norway about 6,000 yr BP; but was, at least in western Norway, not firmly established before the Late Neolithic c. 4,500 – 4,000 yr BP (Myhre, 2004; Hjelle *et al.*, 2006; Høgestøl and Prøsch-Danielsen, 2006). These changes led to a gradual opening up of the forests, lower tree-lines and growth of mountain glaciers (Moe *et al.*, 1996; Nesje *et al.*, 2008). With the spread of agriculture, technological innovations and urbanization, increasingly larger areas became deforested (Rolstad *et al.*, 2001). During the Iron and Middle Ages there seems to be an increase in the use of large scale trapping systems for deer along with export of hides and other animal products (Magnus, 1982; Jacobsen and Andersen, 1992; Mikkelsen, 1994)

DATA COLLECTION AND METHODS

Material

The subfossil material

Almost all subfossil skeletal remains in Norway are stored at the Osteology collections at the University Museum of the University of Bergen and these form the basis for this study. The preservation of bones in open air sites is poor in large parts of Norway and usually only burnt bones are found at such sites (Hufthammer, 2006). Burnt bones may be more resistant to biodegradation (Lyman, 1994), however, the burning process alters the structure and chemistry of the bones causing shrinkage (Shipman *et al.*, 1984) and preventing certain chemical analyses. Caves and rock shelters generally provide a cool and dry environment, which is ideal for the preservation of skeletal remains. The majority of the prehistoric subfossil material in Norway is therefore from such sites. These sites are more numerous along the coast and fjords, and care should therefore be taken when comparing inland and coastal material.

In this study I reviewed all known sites with skeletal remains of moose, red deer and wild boar. Moose and red deer remains have been reviewed before (Ahlén, 1965a; Lie, 1991), but several new sites have been excavated and/or dated since then. Several sites are however poorly documented and I had to perform additional ^{14}C dating of bones from some of these sites to clarify their stratigraphy and age.

Skipshelleren (Bøe, 1934; Olsen, 1976) in Hordaland county is the most important site for this thesis as it is one of the largest, best preserved and documented archaeological sites with subfossil remains of mammals in Norway. This rock shelter site is an ancient human dwelling site situated in a fjord/river valley (Figure 4) in a transitional zone between conifer forests and more broad-leaved vegetation, in the centre of the current Norwegian red deer distribution. The material holds a great variety of species and 23 species of mammals, as well 48 species of birds and 22 species of fish have been identified (Olsen, 1976). The material from this site forms the basis for investigating changes in the relative abundance of species, isotopic analyses and morphological measurements, and constitutes the majority of prehistoric DNA samples.

Figure 4: The rockshelter Skipshelleren (left) and a view of the western Norwegian landscape seen from the site (left). Photos: J. Rosvold.

Contemporary skeletal material

For the morphological investigations I also sampled modern reference material. Most of the skeletons and a large part of the skulls were sampled from the collections at Bergen Museum, which constitute animals from several sites in Hordaland and Sogn & Fjordane counties in western Norway collected between AD 1910 – 1995. Additional skulls were sampled from the collections at NTNU Museum of Natural History and Archaeology originating from the research station at Sognli in Sør-Trøndelag county from animals collected between AD 1956 – 1977. In order to increase the number of female skeletons I also had to obtain partial skeletons from the Norwegian Deer Centre at Svanøy in Sogn & Fjordane. These animals had been shot during regular hunting or killed in traffic accidents in AD 2010 and 2011. The contemporary material thus represents an average of the modern day diversity in skeletal size.

Historic documents

Historic documents were used to trace the presence of the species for the last millennia BP. A search for these was done using library resources and I made use of both zoological literature and old hunting laws. These were studied using both the original copies stored at the Gunnerus Library in Trondheim and facsimile or translated editions of unavailable texts. The oldest broad-scale descriptions of the Norwegian fauna date back to the late fourteenth century AD (Claussøn Friis, 1632, 1881), with some mention also in the work of Olaus Magnus (1982) dated to AD 1555 in Sweden. It should be noted that many of these should be read with care as they are often not based on personal observations or experience and may contain elements of belief, e.g. several sea monsters are described with geographic references. Some of the old known hunting laws of Norway were written down as far back as the early Middle Ages, but probably has oral roots back into the Viking Age (Østlie, 1953). These only describe the economically important game animals.

Quantification and relative abundance of taxa

The quantification of skeletal remains has been an issue of hot debates for a long time (e.g. Reitz and Wing, 1999). Bones are rarely preserved whole in subfossil bone collections and refitting the fragments is usually impossible or too time consuming. There are several ways to quantify the prehistoric abundance of animals by counting bone fragments, like NISP (number of identified specimens), MNI (minimum number of individuals), MAU (minimum number of animal units) and MGUI (modified general utility index); each with its own advantages and disadvantages (Grayson, 1984; Ringrose, 1993; Reitz and Wing, 1999). Of these NISP and MNI are the most frequently used, however Grayson and Frey (2004) have shown that there is usually a high correlation between these measures. NISP is a raw count of the number of skeletal fragments for each species, while most other counts are derived in some way from the NISP. As NISP is a simpler and more replicable way to quantify subfossil bone collections (Grayson, 1984) I have chosen this method for the study.

As an effect of decomposition, butchery and carcass transportation skeletal material from archaeological sites never contains all bones of an animal (Lyman, 1994). There are a range of potential unknown taphonomic factors that may influence subfossil bone collections and there is as yet no way to accurately estimate the absolute abundance of various species through prehistory. The usual way to tackle this is to study the relative abundance of different taxa by comparing species counts. There are, however, several factors that can influence these counts. Sample size may influence the relative abundance of rare taxa in different collections and it is therefore important to account for this relationship (Grayson, 1981; Cannon, 2001). Different species may also differ in the amount of bones in their bodies, bones of larger species may preserve better than small species while larger bones might be fragmented into more pieces, and different species may have been butchered and transported away from the kill site to the collection in differing ways (Lyman, 1994). In addition, hunters may have preferred certain prey over others.

Although, dissimilar in size, moose, red deer and wild boar does have a similar morphology and number of bones in their bodies. Unless locally very rare it is uncommon for large food resources such as these species to be affected by species specific taboos that restricts harvest (Colding and Folke, 1997, 2001). It is therefore likely that any large scale changes in the relative abundance of these species are an effect of real changes in the faunal composition. There is however a real danger that any small changes in the relative abundance is an effect of different taphonomic factors and in such cases (i.e. *paper II*) this was investigated by looking at possible differences in the frequencies of various skeletal parts.

Identifying taxa and the problem of wild boar vs. domestic pigs

Most of the skeletal remains from subfossil bone collections in Norway are highly fragmented due to marrow extraction and trampling. Large parts of a collection therefore remain unidentified to species. Certain skeletal elements, like ribs and vertebrae, are also more difficult to correctly identify to species than others leading to an underrepresentation of such bones. This study is based on the previous taxonomic identifications made by osteologists at the University Museum of the University of Bergen. No attempts were made to identify previously unidentified remains, but identifications were double checked whenever I was working with a material.

Some taxa are, however, difficult to separate from each other and this is especially true of wild boar and early domestic pigs. The wild boar is the ancestor of domestic pigs and they are still regarded as the same species. Early breeds of domestic pigs probably looked very similar to wild boar and, in areas where they co-occured, differentiating their skeletal remains is usually very hard or even impossible based on morphology alone (Albarella *et al.*, 2006; Rowley-Conwy *et al.*, 2012). Geometric morphometric analyses of molars are currently showing promising results in differentiating various populations (e.g. Cucchi *et al.*, 2009) and may prove to be a good method for many cases in the future (Rowley-Conwy *et al.*, 2012). Studying ancient DNA may also reveal introduced lineages of domestic pigs (e.g. Matsui *et al.*, 2005; Larson *et al.*, 2007), however, such analyses have also shown that pigs may have been domesticated locally several times during the Holocene (Larson *et al.*, 2005). Another method, which is independent of lineage, is to investigate dietary changes through an analysis of stable isotopes and this method has given good results in East Asian contexts (Minagawa *et al.*, 2005; Hu *et al.*, 2009).

Using stable isotopes to differentiate wild boar from domestic pigs

In order to map the prehistoric distribution of wild boar in Norway we first had to get an idea of when domestic pigs were introduced (*paper I*). Domestic animals are by definition in close contact with humans and are usually fed additional food by humans, especially during winter. Pigs are omnivores and have as such similar dietary requirements as humans (Powell, 2004). Until modern times pigs were usually held free ranging (Myhre, 2004) and may thus, in addition to being fed waste products, have scavenged human refuse heaps and thereby increased the amount of animal protein in their diet.

Changes in diet can be traced through analysing different stable isotopes, of which ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) are the most frequently used (Peterson and Fry, 1987; Kelly, 2000). These isotopes can be extracted from most kinds of tissues, including subfossil skeletal material (Katzenberg and Harrison, 1997). The ratio of stable isotopes is usually expressed in parts per thousand relative to a standard, e.g.

$$\delta^{13}C = (((^{13}C_{sample} / {}^{12}C_{sample}) / ({}^{13}C_{standard} / {}^{12}C_{standard})) - 1) \times 1000 \qquad [1],$$

which is the PDB limestone formation of South Carolina for ^{13}C (Craig, 1957) and atmospheric nitrogen for ^{15}N (Ehleringer and Rundel, 1989). For animals, differences in δ-values between taxa reflect different diets. $\delta^{13}C$ is dependent on photosynthesis and is primarily used to distinguish different types of plants in the diet, e.g. terrestrial plants from aquatic or C_3 plants from C_4 plants; while $\delta^{15}N$ in animals is enriched compared to their food sources and can be used to trace trophic level (Peterson and Fry, 1987; Kelly, 2000). Domestic pigs fed human waste, including animal products, are therefore expected to differ in $\delta^{15}N$ values from wild boar eating primarily vegetative foods. Ratios may, however, vary between different kinds of tissues (DeNiro and Epstein, 1978; Nardoto *et al.*, 2006) and hence this study (*paper I*) only sampled from tooth dentine. Possible changes in diet due to environmental changes were tested by comparing samples from red deer with the results from wild boar and pigs.

Distribution through time

One of the main aims of this study was to investigate changes in the distribution of the species through time in relation to environmental changes (i.e. *paper I and II*). This was done by mapping the presence skeletal remains of the different taxa through time. As noted above, most of these sites represent archaeological sites and bone collections deposited by humans. The advantage of using such sites is that they usually contain several species and are probably collected from a wide area. We thus also gain some sort of data on the absence of different species. One can, of course, never be sure that the absence of the species in a collection implies that it was not present in the area at that time. However, for important game species as moose, red deer and wild boar, it is reasonable to assume that they were hunted when encountered and that a general lack of a species at least indicates that is was rare in the area. For such a broad scale investigation in both time and space I believe this to be a valid assumption.

Ancient DNA

Ancient DNA (aDNA) from subfossil skeletal remains of red deer was studied (*paper III*) in order investigate in more detail the possible genetic consequences of the historic population reduction and to try to resolve the possibly complex relationship of Norwegian red deer to other populations. Modern methods of molecular phylogenetics have become complex and sophisticated enough to use contemporary genetic information to reconstruct demographic events like changes in population size and migration far back in the past (Lemey *et al.*, 2009). They do, however, rely on several assumptions about past states that may often be hard to verify. aDNA introduces molecular data directly from the past and can thereby be a good way to avoid or test some of these assumptions. aDNA may be particularly useful when the present genetic variation of a taxa is relatively low or when its history might include unknown translocation or hybridization events (Wandeler *et al.*, 2007; Ramakrishnan and Hadly, 2009). It is also the only way to infer exactly what has been lost or gained over time.

This study analyse variation in the control region (D-loop) of mitochondrial DNA (mtDNA) of red deer. mtDNA markers are inherited maternally and are therefore limited to but enable tracing of maternal lineages through time (Moritz *et al.*, 1987). The D-loop is non-coding and has a high evolutionary rate (Brown *et al.*, 1986; Pesole *et al.*, 1999) and is thus a good tool for investigating relationships among closely related taxa (Freeland, 2005). This region is well studied in both Norwegian and European red deer (e.g. Skog *et al.*, 2009; Haanes *et al.*, 2011a), and thus provide ample reference material. mtDNA is also much more abundant than nuclear DNA per cell and thus chances are better that such DNA may be found preserved in subfossil skeletal remains (Hummel, 2003).

The first successful extraction of DNA from an old museum specimen was accomplished in AD 1984 when sequences were cloned from the extinct quagga (*Equus quagga*) (Higuchi *et al.*, 1984), and recently even the near complete genomes of mammoth (*Mammuthus primigenius*) and Neanderthal (*Homo neanderthalensis*) have been sequenced (Miller *et al.*, 2008; Green *et al.*, 2010). Even so, aDNA is still a relatively young discipline and proper protocols often have to be worked out for each project. As soon as an animal dies the DNA in its tissues start decomposing and the degree of DNA fragmentation or presence of PCR inhibitors varies between samples and archaeological sites depending on the environmental conditions (Hummel, 2003; Bollongino *et al.*, 2008).

Lab procedures and population genetic analyses

As the DNA content in old skeletal material is generally very low and fragmented the samples are likely to be contaminated by external DNA from the soil, the excavators or post-excavation handling (Willerslev and Cooper, 2005; Leonard *et al.*, 2007). This is most problematic when studying aDNA from humans or domestic animals, but strong precautions were taken to ensure that authentic DNA was being sequenced (Pääbo *et al.*, 2004; Gilbert *et al.*, 2005), including regular cleaning and change of equipment and working facilities.

The study was initiated by creating proper PCR primers for the region, which were tested on contemporary red deer samples. I chose to work with two overlapping primer pairs in order to reduce the size of the fragments, thereby increasing the chance of successful amplification. In order to produce several copies of what is the most variable region in contemporary animals; primer pairs were designed so as to be largely overlapping. This works as an extra precaution against contamination. I experimented with the various PCR conditions in order to find the optimal settings for the material, generally finding that increasing the amount of DNA extract in the reaction improved the success rate. All samples were sequenced at least twice for each fragment and additional cloning were performed on new haplotypes in order to test for miscoding lesions due to DNA degradation.

Samples from the contemporary Norwegian and western European populations were taken from the literature. Population structure among the contemporary Norwegian populations was tested for using F-statistics (Wright, 1951; Excoffier *et al.*, 1992). The data were divided into four tentative time periods: c. 7,000-3,500 yr BP; 2,500-2,000 yr BP; 1,500-500 yr BP; and contemporary animals. Standard genetic diversity indices were used to investigate changes in genetic diversity through time and Tajima’s D

(Tajima, 1989) and Fu's F_s (Fu, 1997) to look for signs of population expansion or population bottlenecks. I used the Bayesian Skyline Plot (BSP) (Drummond *et al.*, 2005) and the BEAST software (Drummond and Rambaut, 2007) to visualize demographic changes through time and to provide an estimate of substitution rate directly from the aDNA data. In addition, approximate Bayesian computation (ABC) (Beaumont *et al.*, 2002) was used to estimate the magnitude of the historic population reduction as well as to investigate the possibility of any human mediated translocation events. This method was run with and without the aDNA samples to investigate the effect of including such data in the analyses. Relationships between the sequences was tested using several phylogenetic network methods instead of phylogenetic trees, as studies have shown that this better represents the relationship between closely related taxa and highlights areas of uncertainty (Huson and Bryant, 2006; Woolley *et al.*, 2008).

Morphological investigations

The size and morphology of different red deer skeletal elements through time was investigated in order to spot any physiological responses to changing environment (paper IV). The size of an organism defines large parts of its ecology and different body size parameters can reveal several aspects of its environmental adaptations (Lindstedt and Boyce, 1985; Allen *et al.*, 2006; Millien *et al.*, 2006; Yom-Tov and Geffen, 2011). Variations in body size have been linked to changes in climate, nutrition and trophic ecology, as well as competition and predation with results varying between different taxa and environments (ibid.). Body size is a good predictor of metabolism, movement abilities, reproduction and feeding habits of prehistoric animals (McNab, 1990).

In prehistoric animals the only way to study body size is through their teeth and bones, and for many extinct animals this is the only information available at all about their lives. Complete skeletons are rare, but several proxies for body size have been used for fragmented material. Good correlations with ungulate body size have been found for the size and shape of individual molars or breadth measurements of the ends of weight bearing bones (Scott, 1985, 1987; Janis, 1990; Scott, 1990; Mendoza and Palmqvist, 2006). Paper IV analyze changes in 20 osteometric characters on red deer teeth and bones (Figure 5) according to the standards of von den Driesch (1976) and Klein & Cruz-Uribe (1984), but focus on changes in the first and third lower molar (M_1 and M_3) and the astragalus. These three skeletal elements were chosen as they are expected to differ in their responses to environmental change and are among the best represented skeletal elements at the site. All three elements have been found to correlate with body size in cervids (Purdue, 1987; Janis, 1990), however, teeth and bones are expected to differ in their temporal rate of response and the M_3 seems to be more sensitive to changes in diet than the M_1 (Janis, 1990; Solounias *et al.*, 1994).

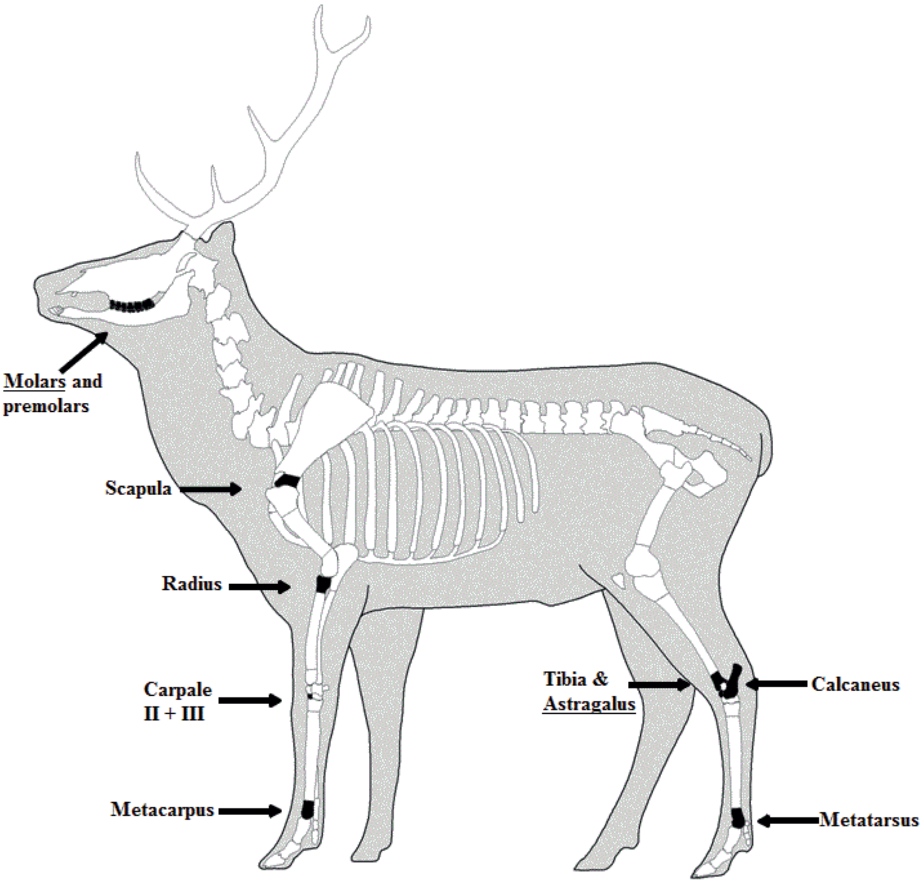


Figure 5: Overview of measured skeletal elements of red deer. Modified from (Yvinec *et al.*, 2007) using a digitalized ArcGIS template by (Orton, 2010).

Prehistoric samples were taken from Skipshelleren and divided into two time periods (Mid and Late Holocene, as above). Contemporary samples were taken from museum specimens collected during the AD 20th century from different areas along the coast. Most of these originate from animals that died prior to the rapid population increase starting around AD 1970. Changes in the size and shape of astragali, M_1 and M_3 were analyzed on a finer time resolution using the average dated layers and transitional layers at Skipshelleren as time points. Thus it was investigated if any changes in size or shape were related to any large scale environmental changes during the Holocene. Analyses were performed on both the complete dataset and mean values for each layer in order to reduce the effects of different sample sizes.

In young growing animals the ends (epiphyses) of the long bones are not fused to the midsection (diaphysis) and bone growth generally stop when their epiphyses are fused (Anderson and Shapiro, 2010). To reduce possible confounding effects of changes in the age structure of the harvest, bones with unfused epiphyses or (for bones lacking epiphyses) a porous structure indicating juveniles were excluded. However, to get an idea of possible changes in the harvest regime a rough estimate of the amount of younger animals were provided by studying the relative amount of fused versus unfused epiphyses in different bones (Mariezkurrena, 1983; Carden, 2006), as well as changes the height of the M_1 which is gradually worn down during the life of an animal (Klein *et al.*, 1981; Nussey *et al.*, 2007; Veiberg *et al.*, 2007). As male red deer are generally larger than females possible changes in the skeletal size measurements could be an effect of changes in sex ratio of the harvest. An estimate of the relative amount of each sex was thus provided by counting the number of sexually identifiable specimens, i.e. canine teeth and pelvis fragments (Lie, 1973; d´Errico and Vanhaeren, 2002; Greenfield, 2006).

RESULTS AND DISCUSSION

A short review of the results

Differentiating prehistoric wild boar from early domestic pigs based on stable isotopes (Paper I)

Pigs and wild boar are notoriously difficult to distinguish from each other based on skeletal morphology alone (Rowley-Conwy *et al.*, 2012). The results from the analysis of ^{13}C and ^{15}N isotopes in subfossil teeth of wild boar and domestic pigs from Skipshelleren support earlier findings from East Asia (Minagawa *et al.*, 2005; Guan *et al.*, 2007) showing that it is possible to differentiate these taxa based on their diet as seen by δ^{15}N values. While no changes in diet is apparent when considering the samples from red deer or the δ^{13}C from wild boar/domestic pig, there is an average shift in δ^{15}N values coinciding with the spread of agriculture. This shift indicate more animal protein in their diet and that the studied Late Holocene *Sus scrofa* remains come from animals eating a diet on average 40 – 60% of a trophic level higher than the Mesolithic wild boar from Skipshelleren. The most likely explanation for this is that these are domestic pigs with access to human refuse. Domestic pigs thus seems to have been introduced relatively early in the Neolithic, but it is unknown if they were domesticated locally or translocated from already domesticated stocks.

Using stable isotopes to differentiate wild from domestic forms of a species is thus a promising method for archaeological assemblages in areas where these could have co-occurred. The differences are expected to be higher for omnivorous species, but should work for any taxa where one might expect a significant dietary change upon domestication. It is however worth noting that the results depend upon establishing a local baseline for the diet of wild animals, as highly different environments or food webs may produce different baselines (e.g. Sealy *et al.*, 1987). In areas were the wild form is extinct this has to be done using subfossil samples old enough to exclude the domestic form and may often require a time series analysis.

Defining the prehistoric habitat of wild boar in Norway (Paper I)

Wild boar was one of the early terrestrial immigrants to Norway, being present from at least 9,000 yr BP. As domesticated pigs may have been present relatively early in the Neolithic (see above) the prehistoric distribution of wild boar can only be inferred from Mesolithic finds, i.e. before about 5,000 yr BP. Based on these results the wild boar seems to have been tied to the southern and western coastal regions of Norway, and wild boar remains are especially abundant at outer coastal sites in areas that contained mast producing trees like oak (*Quercus robur*) and hazel (*Corylus avellana*). The scarcity of central Norwegian sites makes it hard to infer how far north along the coast wild boar appeared, but they did at least reach the Sognefjord. This is the longest of the Norwegian fjords and may be an important dispersal barrier for many species (e.g. Bevanger, 1993; Haanes *et al.*, 2010a). Wild boar are good swimmers, but the fjord is several kilometres wide near the coast and inner parts are mostly surrounded by sheer cliff sides. Genetic studies of red deer also indicate that there is indeed limited dispersal between populations north and south of this fjord area (Haanes *et al.*, 2010a). There are no indications of the presence of wild boar in the inland boreal forests and these areas thus seem to have been unsuitable for any large number of animals. This distribution pattern is in agreement with the northern distribution of subfossil finds of wild boar in Sweden (Ekman and Iregren, 1984; Liljegren and Lagerås, 1993) and Russia (Danilkin, 2001; Danilov and Panchenko, 2012) which are limited to the prehistoric range of broad-leaved forests.

Recently, wild boar has settled in areas with harsher climates than what is found in most of inland Norway today (Markov, 1997; Markov *et al.*, 2005; Danilov and Panchenko, 2012). Considering that climate was warmer during the Mesolithic (Bjune *et al.*, 2005), climatic conditions per se do not seem to have been the limiting factor for the inland dispersal. The results rather support that access to high energy food resources might have limited the northward dispersal and that additional feeding and access to agricultural crops has allowed the wild boar to spread further north today.

Colonization and distribution dynamics of wild lowland ungulates in western Norway throughout the Holocene (Paper I and II)

The distribution of subfossil skeletal remains through time is by necessity coarse, being lumped into periods spanning several thousand years. Several of the sites have uncertain stratigraphic contexts and contain material extending long time periods. A more fine scaled analysis would thus require a large scale direct ^{14}C sampling of bones of each species. The current available information does, however, reveal some interesting patterns.

As expected moose seems to have been the first of the three study species to have colonized Norway during the Early Holocene, with the earliest confirmed presence dated to about 10,300 yr BP (Grøndahl *et al.*, 2010). This is followed by wild boar between 9,900 – 9,000 yr BP (Hufthammer, 2006) and red deer from at least 8,500 yr BP (paper II). All of the earliest sites lie in south-eastern Norway as expected from immigration through southern Sweden. The earliest traces of these animals in western Norway occur after about 9,000 yr BP. In this earliest period these sites are dominated by bones of wild boar and even moose are more abundant than red deer during the Early Holocene. However, during the Mid Holocene warm period (c. 8,000 – 4,000 yr BP) the skeletal material indicates a change in the western Norwegian fauna. Moose remains get scarce while red deer become the dominant ungulate at all sites. Wild boar seems to have remained relatively common during the first half of the Mid Holocene, but towards the end of the period it is harder to infer their distributions due to the possibility of domestic pigs (see above).

During the period c. 4,000 – 1,000 yr BP the relative number of wild boar/pig remains within sites diminish considerably, seemingly in line with the spread of agriculture and loss of the coastal broad-leaved forests. These forests contained trees like oak and hazel that produce high energy foods, which are essential for sustaining the high reproductive capacity of wild boar (Groot Bruinderink *et al.*, 1994; Bieber and Ruf, 2005; Focardi *et al.*, 2008). If food condition deteriorate, only a high adult survival rate has been found to sustain a positive population growth rate of wild boar (Bieber and Ruf, 2005) and the populations may thus have been more sensitive to hunting pressure and stochastic population dynamics. As climate change and human development removed and fragmented large parts of good quality wild boar habitat, agricultural crops may have been an attractive food source. Drawn towards human settlements they would have been an easy target for hunters. Alternatively, this attraction may have facilitated local domestication or interbreeding with introduced domestic pigs. There is no mention of wild boar in Norway in any of the historic documents indicating that they had become extinct as a wild form before or during the Iron Age. Further details on this process may be revealed by studying ancient DNA or geometric morphometrics on wild boar and domestic pig remains.

Contrary to expectations, moose also seem to have become even less abundant in the colder Late Holocene and limited to more inland areas. Red deer, on the other hand, remained common and widespread (but see below). The process of agricultural expansion and forest clearance in western Norway during this period was a gradual process which happened more rapidly in the coastal areas (Kaland, 1986; Prøsch-Danielsen and Simonsen, 2000; Hjelle *et al.*, 2006; Hjelle *et al.*, 2010). Western Norway remained largely forested for a long while, but mostly on the steeper hillsides less favourable to agriculture (Hjelle *et al.*, 2006). Red deer easily make use of steep hillsides and readily adapt to more open terrains (Clutton-Brock *et al.*, 1982) while the more heavily built moose may have been less able to make use of the remaining forest cover. There is no indication that red deer inhabited inland Norway at any time during prehistory and the current spread into these areas might thus be a new phenomenon.

Ancient DNA and the effect of long term population fragmentation and heavy harvest on red deer genetic diversity during the last millennia (Paper III)

Out of 142 subfossil samples 73 (51.4%) were successfully sequenced at least twice for the entire mtDNA region under study. The success rate correlate with the time since the samples were excavated (Figure 6), supporting earlier results which show that handling, post excavation treatment and storage may hasten the DNA degradation process (Pruvost *et al.*, 2007).

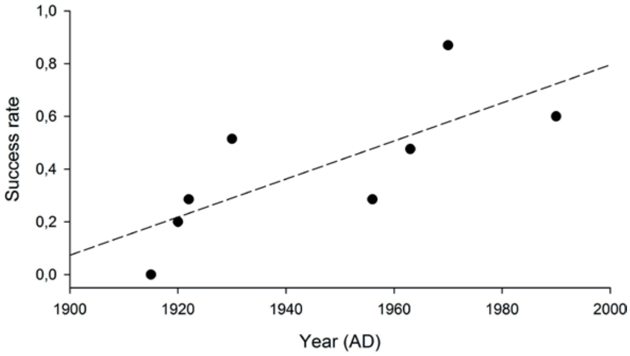


Figure 6: Relationship between excavation year of the site and success rate of DNA amplification (r=0.74, p=0.04).

Compared to the five presently found haplotypes (NO1-NO5) in Norway (Skog *et al.*, 2009; Haanes *et al.*, 2011a) the ancient samples show a higher genetic diversity with ten closely related haplotypes (NO1-NO10, Figure 7). Mid Holocene samples show signs of population expansion while Late Holocene samples dating between c. 2,500 – 2,000 yr BP show the highest diversity indices with seven haplotypes, indicating that the effective population size was high at that time. The data point towards a population decrease starting already in the Iron Age but indicate that it was not as severe as some historic documents seem to imply, thus supporting a previous analysis on contemporary microsatellite DNA (Haanes *et al.*, 2011a). A reason for this might be that although the red deer were reduced to a few small and isolated populations, these populations were scattered over a relatively large area and may thus have represented a large part of the former diversity. The genetic diversity is, however, relatively low among contemporary animals and, even though the current population sizes are regarded as higher than ever, the aDNA data show that at least the effective population size was higher in the past.

Relative haplotype frequencies have changed a lot during the population decline period. Rare alleles or haplotypes are expected to be lost more rapidly during population bottlenecks (Nei *et al.*, 1975). Accordingly, some of the rarest haplotypes among the ancient samples are not found among the contemporary samples. However, surprisingly the most frequent haplotype by far among the ancient samples (NO4) have not been found among contemporary western Norwegian animals but do still occur further north in central Norway. One of the presently found haplotypes (NO3) in western Norway seems to have originated here and become common during this population decline. These changes in haplotype frequencies indicate significant genetic drift during the last two millennia BP. The contemporary populations show a high degree of genetic differentiation, which is a common finding after population fragmentation (Keyghobadi, 2007).

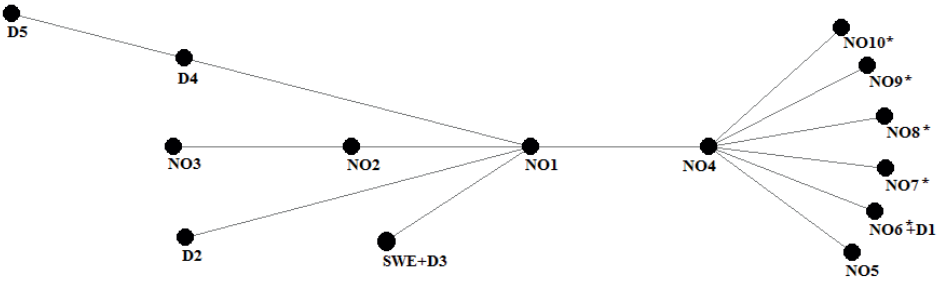


Figure 7: Median-joining network showing the genetic relationship among Norwegian (NO1-NO10), Swedish (SWE) and Danish (D1-D5) red deer haplotypes. *Extinct Norwegian types. Swedish and Danish haplotypes were taken from the litterature (Nielsen *et al.*, 2008; Skog *et al.*, 2009).

The genetic relationship of Norwegian red deer to other populations and the question of its ancestry (paper III)

All the discovered Norwegian haplotypes from the aDNA analysis belong to the western European red deer haplogroup that probably originates from an Iberian Ice Age refugium (Skog *et al.*, 2009). Western European animals are highly related with no apparent phylogeographic structuring. With the inclusion of the ancient Norwegian haplotypes there does, however, seem to be two subgroups within the western European haplogroup, which is also apparent when only studying Scandinavian samples (Figure 7). These centre on NO1 and NO4; both of which are widespread in western Europe, and could possibly indicate different glacial refugial areas within Spain and southern France. Gyllensten *et al*. (1983) found signs of a possibly closer relationship between Scottish and Norwegian animals than with Swedish. However, they only studied central Norwegian animals which are highly dominated by the haplotype NO5 and to some degree NO4. Swedish red deer may have been more severely reduced in numbers as only one haplotype (closely related to NO1) has been found among the original stock (Skog *et al.*, 2009; Haanes *et al.*, 2011a). An analysis of aDNA from Swedish samples may thus be required to shed more light on the relationship and contact between Scandinavian deer through time.

The aDNA data show that among the five presently found mtDNA haplotypes (NO1-NO5) of Norwegian red deer all but NO3 have been found among samples dated to 2,000 yr BP or older, i.e. long before any suspected translocations of red deer into Norway. The haplotype NO3 has so far only been found in Norway and is highly related to NO2 (Figure 7) which also seems exclusively Norwegian. It is thus more likely that this haplotype has originated in Norway and become common today as an effect of genetic drift. The ABC analyses support this by indicating just one colonization event. One cannot exclude the possibility that humans may have translocated animals in earlier times, as seems to be the case for the Irish red deer already in the Neolithic (Carden *et al.*, 2012). Considering the high abundance of red deer remains in western Norway since the early Mid Holocene (paper II), the reason for doing this seems unlikely. The results in paper III only consider the female lineage, but based on that there is no evidence of any human mediated translocations of red deer into Norway. Apart from a small introduction of Hungarian animals to the island Otterøya around AD 1900, which does not yet seem to have spread outside the island (Haanes *et al.*, 2010b), the Norwegian red deer may be one of the few European populations free from human mediated admixture.

Late Holocene morphological changes in the skeleton of red deer (paper IV)

The morphological investigations on the skeleton of red deer show that the prehistoric Norwegian red deer was much larger than today. Judging by the size of the astragalus, and assuming that the animals were as sexually dimorphic as they are today, the skeletal size of contemporary males is similar to small prehistoric females. The measurements of prehistoric deer from Skipshelleren are on average 6.7 – 17.3 % larger for bones and 12.5 – 17.4 % larger for teeth than of contemporary animals, with little size overlap. The measurements of most weight-bearing bones and molar breadths indicate a stable body size through time within the period covered by Skipshelleren (c. 7,100 – 1,800 yr BP) and a large reduction sometime within the last two millennia BP. Tooth lengths (Figure 8) show a continuous decrease throughout the study period, possibly reflecting a slow and ongoing adaptation to the Holocene environment. However, this decrease was accelerated during the last 2,000 years. There are also indications that the crown heights of the molars have been reduced through time. Several studies indicate a strong genetic component in determining the size and shape of teeth (Bader, 1965; Townsend and Brown, 1978; Fortelius, 1985; Hillson, 1986). It is thus expected that post-cranial bones show more plasticity than teeth, and dwarfed mammals often retain large teeth relative to their body size (Gould, 1975; Lister, 1996). Interestingly the results show that the teeth have been reduced in size as much as or even more than post-cranial weight bearing bones, with the largest decrease in the first lower molar (M_1). This indicates a strong selection for smaller size during the last two millennia BP.

Body size in homeotherms is generally expected to vary with climate (Mayr, 1956; Gardner *et al.*, 2011), either through physiological adaptations (e.g. Mayr, 1956; Lindstedt and Boyce, 1985) or through the effects of climate upon food availability and quality (e.g. Langvatn and Albon, 1986; McNab, 2010). Surprisingly, there is no indication that the climatic cooling between the Mid and Late Holocene had any noticeable effect upon the skeletal morphology of Norwegian red deer. The proportionally equal or larger reduction of the teeth compared to weight-bearing bones is also in contrast to the idea that red deer became more of a grazer during the Late Holocene, due to the widespread loss of forests, as grazers generally have larger occlusal surface area and larger crown heights relative to their body size (Janis, 1990;

Solounias *et al.*, 1994; Pérez-Barberia and Gordon, 2001). The large reduction in both teeth and bones during the last 2,000 yr BP happened during a period of large-scale human mediated habitat alteration and fragmentation, increased populations of domestic herbivores and heavy hunting. It is thus likely that several human-mediated factors were responsible for the size reductions in red deer. Little skeletal material is as yet available for studying size changes within these last 2,000 years BP, but this may at a later time provide important information on the factors responsible for the decrease.

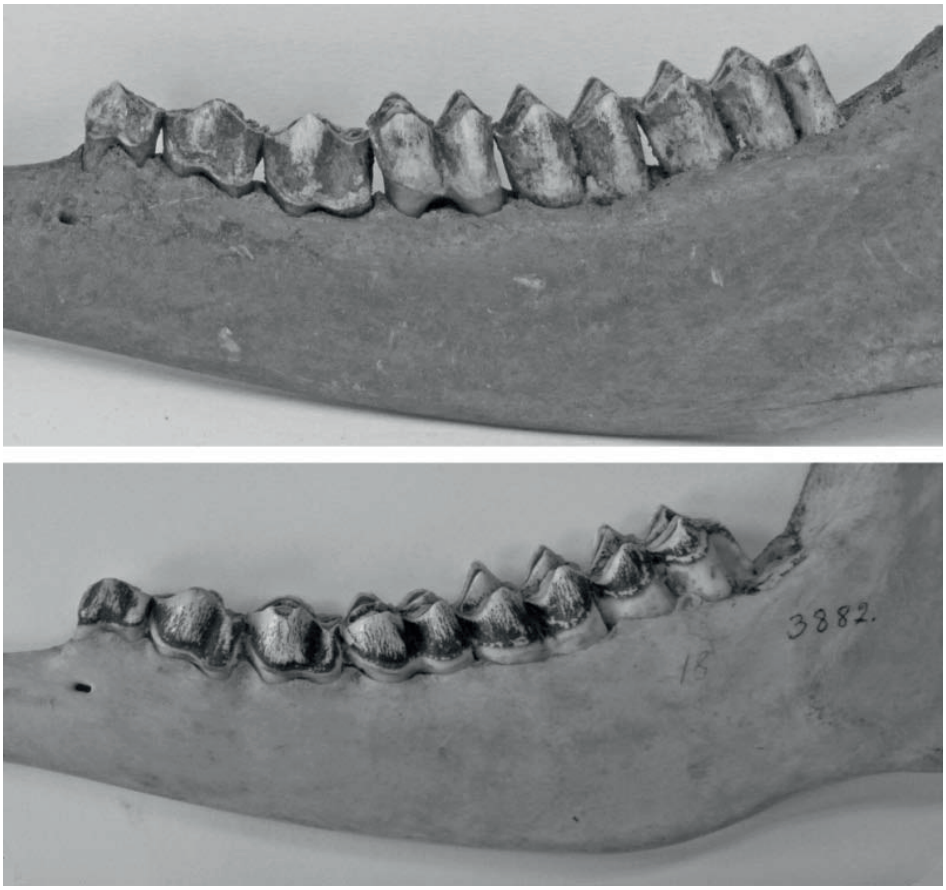


Figure 8: Lower left jaws and cheek teeth of prehistoric (above) and contemporary (below) Norwegian red deer. The images are scaled to illustrate the approximate size difference between prehistoric and contemporary animals. Contemporary animals typically show more crowded teeth and often have a reduced third cusp of the M_3. Photos: Jørgen Rosvold.

The history of western Norwegian ungulates in a social-ecological context

The results from the above studies (paper I-IV) indicate that the history of ungulates in western Norway is a result of a number of interacting ecological and cultural/social factors changing through time. Ungulates have interacted with humans for a long time and their dynamics must therefore be understood through changes in the social system of humans as well, i.e. in a social-ecological system (Berkes and Folke, 1998). The importance of this is illustrated by the fact that most of the material used in this study is the result of human hunting through time. Integrating social and ecological factors adds complexity to the interpretations, but is important in order to understand how both nature and human society has evolved during the last millennia. In order to put some of the above results into a context that may shed some light on the current and future situation of wild ungulates, I have taken the "adaptive cycle" approach of Holling (2001). The adaptive cycle characterize changes in social-ecological systems through four phases: r, K, Ω and α. The first phase of the cycle is the growth or exploitation phase (r), which is characterized as a pioneer phase with readily available resources for opportunists and the emergence of new connections. The cycle proceeds slowly towards a conservation or consolidation phase (K), which is characterized by increasing structure and connections within the system, and an increase in capital. However, the system also becomes less flexible, as more resources are bound up, and more vulnerable to disturbances, i.e. less resilient. This process can be compared to ecological succession, e.g. a transition from pioneer vegetation to climax forest. The release phase (Ω) is initiated by a disturbance, e.g. forest fire or a breakthrough innovation, and signify a collapse of the old organization and connections. This is quickly followed by the reorganization phase (α) in which the cycle may be repeated or change into a new regime. For a thorough review see Gunderson & Holling (2002). In such a view the Holocene history of wild ungulate exploitation in western Norway can broadly be summarized into three large-scale regimes: the "wild ungulate regime" (c. 11,500 – 4,000 yr BP), the "domestic ungulate regime" (c. 4,000 – 100 yr BP) and the "management regime" (contemporary and future time).

The wild ungulate regime (c. 11,500-4,000 yr BP)

Due to the Last Ice Age, ending about 11,500 yr BP, the history of terrestrial animals in Scandinavia is relatively young. The western coast of Norway was probably ice free well before this, but the southern land passage from continental Europe was blocked by ice and sea (Andersen, 1980; Mangerud *et al.*, 2011) until about 11,000 yr BP when a land bridge connected the Scandinavian peninsula and continental Europe (Björck, 1995). With the aid of boats, humans had settled along most of the coastline before 11,000 yr BP (Bjerck, 1995; Bang-Andersen, 2012), subsiding on reindeer hunting and marine resources (Bang-Andersen, 1996; Bjerck, 2009; Bang-Andersen, 2012; Fuglestvedt, 2012). These people may be defined by a high degree of mobility, leaving traces of their presence mostly in open air sites containing little organic remains (Nygaard, 1989; Bang-Andersen, 2003; Bjerck, 2008). This mobility may in part be a reflection of the highly dynamic environment of the Early Holocene. Temperatures were increasing, causing the ice to retreat inland and eventually disappear, leading to rapid changes in the shorelines due to rising sea levels and/or land uplift (Andersen, 1980; Nesje and Kvamme, 1991; Anundsen, 1996). The vegetation was going through different stages of succession from arctic pioneer vegetation, to birch and pine dominated forests and eventually temperate deciduous forests along the coast (Moe *et al.*, 1996). The immigration of moose, wild boar and red deer was part of this environmental change and they entered a land already inhabited by humans.

The end of the Ice Age represent a reorganization of the ecosystem along western Norway, open to new social-ecological connections and innovations, corresponding to the α phase of the adaptive cycle (Holling, 1987; Holling and Gunderson, 2002). Likewise, the Early Holocene (c. 11,500 – 8,000 yr BP) represents the *r* phase of this emerging system, with colonization and succession of new biota and new resources for the humans. Not surprisingly, the moose seems to have been the first of the three study species to have colonized Norway (paper II). Moose are well suited for such a rapid exploitation of newly available land as they are well adapted to the northern environment, both males and females may disperse over long distances, and they have a relatively high reproductive potential (Andersen and Sæther, 1996; Ball *et al.*, 2001; Gaillard, 2007). However, as the climate got warmer and the climax forests were established in the Mid Holocene, the moose retreated inland (paper II). Due to its high reproductive rate and opportunistic population dynamics the wild boar has a large potential for population expansion (Bieber and Ruf, 2005) and was the next of the three to colonize Norway (paper I). The wild boar may have followed the spread of hazel along the coast and had fewer competitors for such resources during the early Holocene. Unlike the moose, wild boar also thrived in the Mid Holocene coastal broad-leaved forests (paper I). Red deer seems to have been a late successional species which became common in western Norway along with the spread of the climax forest (paper II). However, once established it would eventually become the most important terrestrial prey of humans.

It is possible that the presence of humans affected the spread and establishment of these species, but the Early Holocene material is yet too scarce to provide such information. It is commonly assumed that the overall density of humans at that time was too low to have had any large impact on most other species. However, in a naturally fragmented landscape, like western Norway, the overall human density need not be large in order to affect the animals if their influence is high in certain key areas, like migration corridors, important winter habitats or breeding areas. On the other hand, it is likely that the immigration of these "alien" species affected the ecology and social system of the humans in many ways. An increasingly wider range of available prey and plant resources may have created a more steady supply of local resources and thus facilitated enlarged human populations and increased residential stability (Harpending and Davis, 1977), which is observed during the Mesolithic and Neolithic (Indrelid, 1978; Nygaard, 1989; Bergsvik, 2001; Bjerck, 2008). Later this would have been reinforced by the introduction of another set of ungulates; the domestic ones. Compared to the rest of Europe, the establishment of agriculture and animal husbandry was a more gradual process in Northern Europe (Zvelebil and Rowley-Conwy, 1984), including western Norway (Bakka and Kaland, 1971; Prescott, 1996; Hjelle *et al.*, 2006). Agriculture and domestic animals seems to have been introduced early in the Neolithic but was not properly established before about 4,500 – 4,000 yr BP (Hjelle *et al.*, 2006; Høgestøl and Prøsch-Danielsen, 2006). The establishment of the denser Mid Holocene forests and the progression from a mobile hunter/fisher organization to a more sedentary way of life, and thus a heavier reliance on local resources, represents the slower transition from the *r* phase to the *K* phase of ungulate exploitation. The transition from a hunting economy to a more agrarian economy has been widely discussed and probably involves a range of social factors (Bakka and Kaland, 1971; Zvelebil and Rowley-Conwy, 1984; Prescott, 1996; Myhre, 2004; Hjelle *et al.*, 2006). The climatic cooling at the end of the Mid Holocene (Bjune *et al.*, 2005) coincides with this transition and may also have been an important part of this process. It is, however, clear that these changes led to a new ungulate regime in the western Norwegian ecosystem. The Ω phase and the transition to this new regime thus include both climate change and an increased reliance on local resources, with subsequent effects upon the vegetation.

The domestic ungulate regime (c. 4,000-100 yr BP)

The climate cooling of the Late Holocene led to a re-emergence of mountain glaciers (Nesje and Kvamme, 1991; Nesje *et al.*, 2008), lower tree-lines and more open forests with less thermophilous plants (Moe, 1979; Aas and Faarlund, 1988; Moe *et al.*, 1996; Bjune, 2005). The increased dependence on domestic ungulates and agriculture meant that the forests were now more of a limitation for humans and was thus cleared to make way for new fields and pastures. In many ways these actions had the effect of strongly enhancing the vegetation changes caused by the colder climate. The clearing of the coastal forests transformed the landscape into open grass or heathlands (Kaland, 1986; Prøsch-Danielsen and Simonsen, 2000; Hjelle *et al.*, 2010) and summer farms in the mountains suppressed the tree-lines even further (Moe *et al.*, 1996; Bjune, 2005). The most productive soils were often the ones to be developed first (Overland and Hjelle, 2009; Hjelle *et al.*, 2010) and wild ungulates may thus have been excluded from important foraging areas. Good quality leaves and graminoids were gathered as winter fodder for livestock (Austad *et al.*, 2001; Hjelle *et al.*, 2006), which may have decreased food availability for wild ungulates during winter.

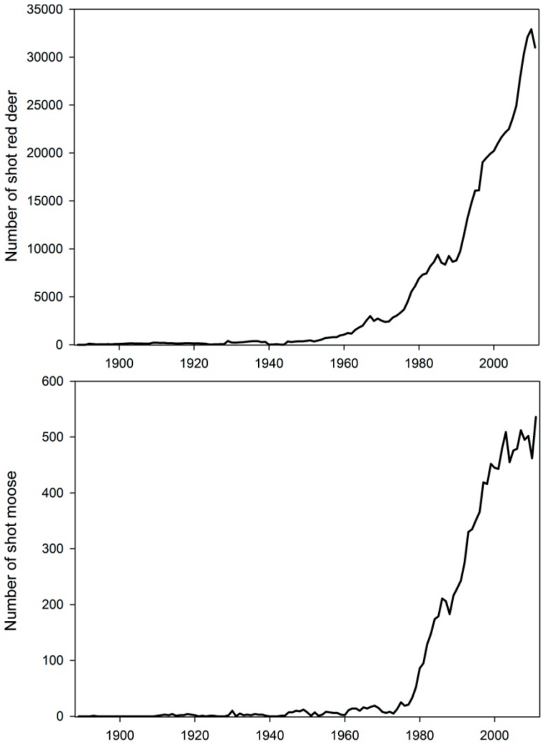
Like the Early to Mid Holocene succession, the Late Holocene process of domestic ungulate dominance, forest clearance and habitat fragmentation was a gradual process which was accelerated through time due to an increasing human population, iron production, mining, salt boiling and timber export (Rolstad *et al.*, 2001), i.e. a progression from *r* to *K*. This new landscape was in favour of domestic ungulates and a grazing regime. The continued high abundance of bones of wild ungulates and other wildlife in archaeological sites show that hunting remained an important part of the economy (Hufthammer, 1995; paper II) and has been so up until modern times (e.g. Jacobsen and Andersen, 1992; Sølien, 1995). However, as livestock became an increasingly important part of the economy wild ungulates became more of a subsidiary resource, although still important and a good resource for trade. Livestock and agricultural products provided a more stable and controllable food source, and human population dynamics would thus have been more independent of changes in the populations sizes of "wild" resources and more able to over-exploit them (e.g. Winterhalder and Lu, 1997). Growing human populations and technological advancement increased mobility and foreign contact, giving rise to an increased market for animal products. Trade in hides and antler products seems to have been large already during the Iron Age (Mikkelsen, 1994; Solberg, 2000) and especially during the Middle Ages and onwards (Collett, 1912; Magnus, 1982; Mikkelsen, 1994).

Some species, like wild boar and moose seems to have been affected quite early in this increasingly agrarian context. Wild boar eventually became extinct, at least in its wild form (paper I). Moose was suppressed to more inland areas and probably isolated from the larger populations east of the mountains due to restricted migration corridors (paper II). Red deer, on the other hand, managed these changes better than wild boar and moose (paper II – IV). There are no discernible impacts on the distribution of bone finds (paper II), genetic diversity (paper III) or the physical stature (paper IV) of red deer until the Iron Age, about 2,000 yr BP. Red deer is more of a grazer than wild boar and moose, and prefer foraging in forest glades and meadows (Mysterud *et al.*, 2002; Godvik *et al.*, 2009; Kuijper *et al.*, 2009). Early phases of forest clearance may thus have been positive for red deer by creating new pastures and improved forage in close connection to shelter. Some degree of grazing by domestic herbivores may also facilitate foraging for red deer (Gordon, 1988; Rhodes and Sharrow, 1990; Mysterud *et al.*, 2011). However, as the new regime progressed deeper into the agrarian system, the red deer as well seems to have suffered reduced living conditions as indicated by reduced genetic diversity (paper III) and body size (paper IV).

The AD 19th and the early 20th century represent the Ω phase of this regime. Already in the AD 16th century concerns were expressed about the state of the Norwegian forests and the standing cubic mass likely reached their lowest levels around AD 1900 (Rolstad *et al.*, 2001). This lead to increased management of the forests and widespread replanting (Rolstad *et al.*, 2001; Almås, 2004). Older texts states that red deer had become a rare sight in western Norway in the AD 17th century (Claussøn Friis, 1632; Pontoppidan, 1753; Strøm, 1762) and was in the AD 19th century reported to consist of only a handful of small and isolated populations spread along the coast (Collett, 1909). Strong hunting regulations was consequently enforced (Østlie, 1953), leading to today's management regime. The number of large carnivores was reported to be especially high during the AD 18th and 19th centuries (Collett, 1877). We know little of the changes in predator abundance during the Holocene, but it is possible that the perceived increase was due to the lower abundance of wild ungulates which may have forced the large carnivores into closer contact with humans. The threat to domestic animals and the concern for the low abundance of game animals was among the reasons for a large scale politically initiated campaign for reducing carnivore numbers in the AD 19th and early 20th century (Sølien, 1995). Together with industrialization and agricultural reorganization, these factors led to new conditions for wild ungulates.

The management regime (contemporary and future time)

Throughout the last century there have been large changes in the Norwegian landscape, which are largely ascribed to a reorganization of the Norwegian subsistence and strong economic growth. These changes in the social system involve a range of factors, e.g. globalization, industrialization and environmentalism, which are beyond the range of this thesis. It is, however, clear that this led to a reorganization of the social-ecological system involving ungulates. Strong economic growth, caused by e.g. shipping industry, marine exploitation, hydro power and the discovery of oil, as well as a reorganization and industrialisation of the agricultural system has reduced both the relative amount of people needed for and dependent on agricultural activity (Almås, 2004). While the total amount of domestic ungulates is still high, the use of outfields for grazing has been greatly reduced (Almås, 2004; Austrheim *et al.*, 2008; Austrheim *et al.*, 2011). Forest management and the reduction of outfield livestock grazing has led to a rapid re-growth of forests during the last century (Rolstad *et al.*, 2001; Almås, 2004), and at the same time both temperatures and tree-lines have been rising (Aas, 1969; Aas and Faarlund, 1995; Dalen and Hofgaard, 2005). Hunting of ungulates has continued to be important, but more in the form of recreational hunting, and management has focused on maintaining a high growth rate of the populations by restricting the hunting season and the amount of adult females being shot (Andersen *et al.*, 2011).



Figur 9: Number of registered shot red deer and moose in western Norway (Rogaland, Hordaland, Sogn & Fjordane and Møre & Romsdal counties) per year between 1889 and 2011. Data from Statistics Norway.

The number of red deer in western Norway has had an almost exponential increase during the last century (Figure 9), with the largest increase since the AD 1970s. Current estimates suggest that the total Norwegian stock consist of about 150,000 animals (Pedersen, 2009). This high density may be unprecedented and part of the reason why red deer is increasingly observed also in inland eastern Norway. In line with a similar rapid increase in inland moose populations (ibid.), the number of moose in inner parts of western Norway has also been increasing during the last 30 years (Figure 9). Wild boar, on the other hand, has not yet returned. The Swedish populations of wild boar persisted much longer than the Norwegian, but were exterminated during the AD 18th century (Ekman, 1922). They were later reintroduced to fenced areas, from which they managed to escape, and has had an explosive population growth during the last 20 years (Lemel and Truvé, 2008). These animals have now started crossing the border into Norway (Haaverstad,

2011) and, if unhindered, is expected to find good habitat conditions also in western Norway in the future (Rosvold and Andersen, 2008).

Future climate is expected to be both warmer and wetter than today (Hanssen-Bauer *et al.*, 2003; Engen-Skaugen *et al.*, 2007) with increased length of the growing season (Førland *et al.*, 2004; Skaugen and Tveito, 2004) and increased distribution of thermophile plants (Sykes and Prentice, 1995). We thus seem to have entered the *r* phase of a new ungulate regime that in many ways seem similar to the old "wild ungulate regime". There are, however, some important differences that set this regime apart: e.g. the human population size is large; agriculture is still present; the forest structure is likely different due to the modern practice of clear-cutting and re-growth; large non-human predators are rare; the genetic diversity of at least red deer is reduced; and we have a strong management system. We seem to be moving towards a state where neither wild nor domestic ungulates, at least locally produced, are a necessity for the subsistence of the majority of the people. However, the pervasive human control of the ungulates has caused some to question whether the wild ungulates can still be called "wild" (e.g. Mysterud, 2010).

Conclusions

The three regimes outlined above are rough in scale and scope. Many events that are not considered here have likely taken place within these regimes. The subsistence of humans in western Norway seems always to have been highly maritime oriented, thus changes in marine resources may also have affected the use of terrestrial resources. The three regimes do, however, illustrate three periods in the history of western Norwegian large ungulates with important differences in environmental factors influencing the animals. These regimes may serve as a basis for further studies which could identify more short-term cycles within each regime and provide details on the transition between them. Similar broad-scale changes in climate and human exploitation of land and ungulates may have happened in large parts of the world (e.g. Bradshaw, 1999) and, although timing and magnitude of different factors will vary, the three regimes outlined above may well fit a wider context.

The above results illustrate that the western Norwegian fauna and landscape has been changing in several ways ever since land emerged from the ice for more than 11,000 years ago. They also show that humans have been influencing wild ungulates for a very long time. Indeed, humans were present long before moose, wild boar and red deer appeared in Norway and has thus experienced the colonization of several "alien" invasive species. Many consider the "human factor" on natural systems to be negligible until the last few centuries and the industrial revolution. It is, however, becoming increasingly clear that our "footprints" are noticeable far back in the past all over the world (e.g. Schüle, 1992; Burchard, 1998; Shotyk *et al.*, 1998; Marziani and Citterio, 1999; Prøsch-Danielsen and Simonsen, 2000; Grayson, 2001; Burney and Flannery, 2005; Briggs *et al.*, 2006; Bayon *et al.*, 2012). The consequence of this is that there is no point in going back in time to find a more "natural" state. Humans should rather be included as part of this dynamic system (Head, 2008). This dynamic view of nature also leads to the question about what defines an alien invasive species (Warren, 2007; Gillson *et al.*, 2008). E.g. why are wild boar considered alien while roe deer, which seems to have been very rare in prehistory and only migrated to Norway around 100 years ago (Collett, 1877; Andersen *et al.*, 2004), are considered native? Rather than maintaining a stasis the focus should be on maintaining the ability of species and systems to adapt and evolve, e.g. by maintaining possibilities for migration and preserving genetic diversity.

"*Preserving nature is not about stasis, but about maintaining the exciting, ever-evolving variety of life on Earth*"

Sandra Knapp (2003)

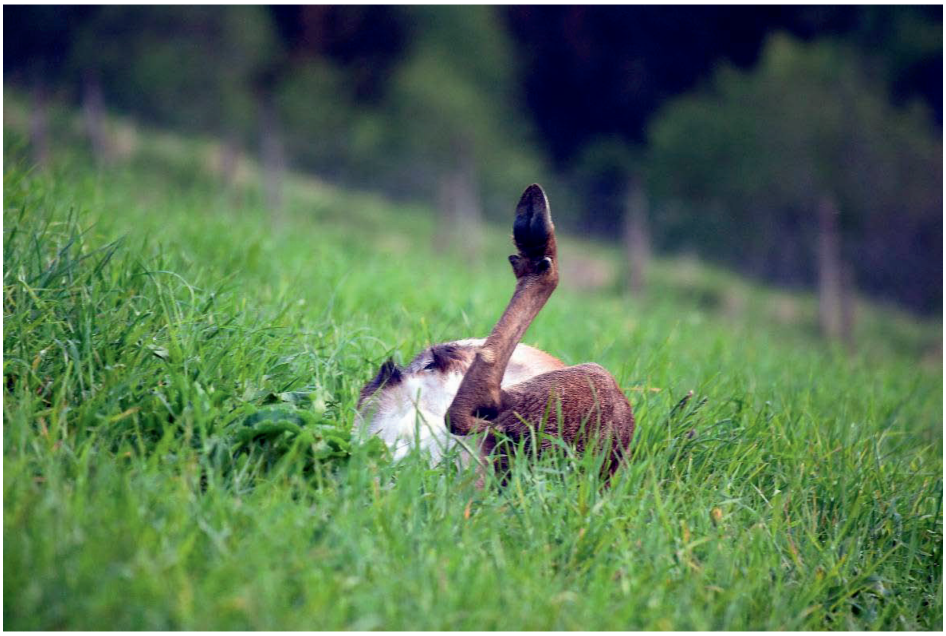


Photo: © Johan Trygve Solheim, Norsk Hjortesenter

GLOSSARY

^{14}C date vs. calendar date: organic material can be dated fairly precisely by measuring the amount of the unstable carbon isotope ^{14}C it contains relative to the atmosphere. When an animal is alive the level of ^{14}C incorporated in its body is similar to the level in the atmosphere, but when it dies this fraction declines with time at a fixed rate. However, the level of atmospheric ^{14}C has not remained constant through time, meaning that the age measured by the level of ^{14}C is not identical to calendar years and has to be calibrated.

Allele: Variants of a particular gene.

Anthropogenic: Created or caused by humans.

Archaeozoology: The study of animals using archaeological material.

Biota: The total collection of organisms in an area or time period.

BP: Before present. Here given in calendar years.

Bottleneck: A sharp temporary reduction in the effective population size which may lead to reduced genetic diversity.

Effective population size: The number of adults who contribute with offspring to the next generation in a population. In population genetics it is defined as the size of an ideal population loosing genetic diversity at a rate equal to that of the observed population. It is usually lower than the actual population size due to effects such as unequal sex ratio or fluctuating population size.

Genotype: A particular set of genes in an individual.

Geometric morphometrics: Multivariate study of shape in two or three dimensions.

Haplotype: A particular form of a DNA sequence.

Haplogroup: A group of similar haplotypes that share a common ancestor.

Holocene: The current geological epoch which began about 11,500 years ago following the Last Ice Age.

Isotopes: Variants of particular chemical element, differing from each other by the number of neutrons in the nucleus of the atom.

Mesolithic: In Norwegian archaeology refers to the Older Stone Age, i.e. before the introduction of agriculture.

mtDNA: DNA which is found in the mitochondria of cells and not in the nucleus. It is usually only inherited maternally.

Neolithic: Refers to the Younger Stone Age, i.e. after the introduction of agriculture.

Occlusal surface area: The area of the teeth that is in contact with the corresponding teeth in the opposing jaw, i.e. the chewing surface.

Osteology: The study of skeletal elements; their form and function.

Osteometry: Measurements on the skeleton.

Phenotype: An expressed trait, e.g. colour, size, shape, behaviour. This trait is the product of a particular genotype, the environment and the interaction between genotype and environment.

Phylogenetics: The study of evolutionary relationships among taxa.

Phylogeography: The study of evolutionary relationships across geographic space in order to understand which processes have shaped the spatial distribution of taxa.

Refugium: An area occupied by a population during a period of restricted distributions, e.g. during an Ice Age for temperate species.

Rockshelter: Cave like opening at the base of a cliff. Rocky overhang or inclining cliff side often used as dwelling site. The difference between a cave and a rock shelter is often blurry.

Subfossil: Remains where the fossilization process in not yet complete, i.e., organic material still remains.

Ungulate: A mammal with hooves.

Taphonomy: The study of the transition of information from the living community to the studied fossil or subfossil collection and factors that may alter this. It includes factors such as excavation bias, decomposition, scavenging, butchery practices etc.

Taxon: A unit of organisms being studied. E.g. a population, a group of populations, a species etc.

Trophic level: The position of an animal in the food chain.

Typology: In archaeology is a classification of artefacts with the purpose of spotting relationships and development. Can be used to date archaeological sites.

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Paper I

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Paper II

Cervids in a dynamic landscape: Holocene changes in moose and red deer abundance along the limit of their distribution

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Abstract

Future climate change is believed to have a strong potential impact on the distribution of large ungulates on a regional scale. At the same time, changes in human land use on a more local scale may affect their distribution and dispersal abilities, possibly confounding the effects of climate. Here we analyse changes in the Holocene distribution and relative abundance of moose and red deer skeletal remains along a sympatric range boundary of these species in western Norway. As moose and red deer are adapted to different climatic conditions we would expect the distribution of finds to reflect large scale changes in climate. In accordance with this prediction our results indicate that red deer became the predominant ungulate in this area during the mid Holocene warm period. Contrary to this, remains of moose became even less abundant in the subsequent colder period. This decrease seems tied to the spread of agriculture and deforestation, indicating the importance of considering changes in land use when predicting future changes in ungulate distribution.

Keywords: *Alces alces*, *Cervus elaphus*, Holocene, western Norway, climate change, agriculture, Skipshelleren

Introduction

The distribution of species is not a fixed arrangement but changes through time in response to environmental changes. Climate, directly or indirectly, is considered as one of the main driving forces of such changes, pushing species south during cold periods and north during warmer periods (Graham, 1986; Webb and Bartlein, 1992; Hofreiter and Stewart, 2009). Several studies indicate that this is an ongoing process in most natural systems today (eg, Walther *et al.*, 2002; Root *et al.*, 2003). However, differences in dispersal ability and adaptability will lead to species specific responses to climate change and may thus cause changes in community structure over time (Graham, 1986; FAUNMAP Working Group, 1996).

The effects of environmental change can be expected to be most pronounced at the distributional limits of a given species (Haldane, 1956; Williams *et al.*, 2003). Southern Norway is currently a border zone between the distributional limits for moose (*Alces alces*) and red deer (*Cervus elaphus*). The historical distribution of the red deer in Norway has been along the milder west coast while moose have been mainly associated with the more continental eastern inland, with the species being separated by the Scandes mountain chain (Collett, 1912). Although there is some range overlap, moose and red deer can be considered as allopatric species on a global scale (Ahlén, 1965; Mitchell-Jones *et al.*, 1999). This distribution pattern, with moose mainly being limited to the boreal taiga and red deer to the temperate forests, indicates that they are adapted to different climatic conditions. Moose have a body construction well suited for movement in deep snow (Formozov, 1946; Telfer and Kelsall, 1979) and are able to withstand periods of extreme cold, but are easily stressed by high temperatures both in summer and winter (Markgren, 1966; Renecker and Hudson, 1986; Lenarz *et al.*, 2009). Red deer on the other hand, although highly adaptable, are not as tolerant of cold (Simpson *et al.*, 1978; Semiadi *et al.*, 1996) or snowy conditions (Formozov, 1946; Ahlén, 1965). They are also more dependent on grazing and have problems feeding if they cannot reach the ground vegetation (Ahlén, 1965; Mysterud *et al.*, 2001). Thus, changes in the relative abundance of these two species could be expected to directly or indirectly reflect climatic conditions.

Largely attributed to changes in human land use and wildlife management practices many wild ungulates, including moose and red deer, have been increasing in numbers and distribution in Europe during the last century following earlier dramatic population declines (Linnell and Zachos, 2011). Through high hunting pressure, game management, translocation of animals and habitat alterations human activities have grown to become a dominant factor in the environment of wild ungulates (Mysterud, 2010; Linnell and Zachos, 2011), and may have become more important than climate in structuring their distribution and movements. The Holocene record of moose (Schmölcke and Zachos, 2005) and red deer (Sommer *et al.*, 2008) in central Europe show that their prehistoric distributions were more sympatric than today, highlighting both climate and humans as potential factors in structuring their ranges.

Here we expand upon this by investigating changes in the distribution of moose and red deer along a distribution boundary for these species in a long-term perspective. We do this by looking at the distribution of subfossil bone finds from the Holocene (the last 11,500 years) in western Norway, and a more in-depth study of changes in the relative abundance of moose to red deer at the archaeological rock shelter site Skipshelleren for which the bone record is particularly rich. Following the Last Ice Age, there have been considerable climatic fluctuations (i.e. Nesje and Dahl, 1993), and our hypothesis is that these would have affected the relative distributions of moose and red deer. If so, we predict that moose bones would be relatively less abundant in archaeological sites dated to warmer periods of the Holocene and more abundant during the cooler periods. Human land use may however have influenced these changes, and we discuss the results in light of current knowledge on the development of Late Holocene agricultural activity and deforestation.

Study area

The Scandes mountain range makes a natural barrier of alpine tundra between eastern and western Norway, in many parts reaching out to the coast creating long and narrow fjords with steep hillsides (Figure 1). This creates a highly varied topography in western Norway with equally varied local climates and vegetation (Moen, 1999). The coastal areas and fjords are mild and wet for most of the year and low elevations usually receive very little snow. Higher lying areas have more pronounced climatic fluctuations with longer and more snow rich winters. Presently, overall precipitation decreases eastwards but snow cover increases and may reach considerable depth in some areas during winter (October-April). Annual temperatures range from about 8 °C on the western coast to -6 °C in mountainous areas. Broadleaf forests cover parts of the coast, but the outer coast is characterized by treeless coastal heathlands. Further inland mixed coniferous and deciduous forests changes to more boreal vegetation.

The rock shelter Skipshelleren (site 19 in Figure 1) is an ancient human dwelling site containing one of the largest and best stratified subfossil faunal collections in Norway. It lies in a transitional zone between coniferous forest and more broad-leaved vegetation. Skipshelleren is situated in a fjord/river valley leading about 35 km inland to Voss, which presently has a small but stable moose population. Only a few straying moose are at times observed near the site, but the area presently supports a large population of red deer (Overvoll and Wiers, 2004).

Material and methods

Distribution analysis

Almost all subfossil bones of moose and red deer in Norway stem from archaeological excavations of human dwelling sites, mostly caves and rock shelters, and are stored at the Osteology collections at the University Museum of the University of Bergen. We reviewed files from the collection archive, published papers and publicly available archaeological reports and theses with subfossil remains of moose and red deer in western Norway and adjacent mountain regions. Those samples which were found to be securely dated, either by ^{14}C or typology, were used in the analysis (Appendix A). Skeletal material worked into tools was excluded as these may have been more subject to long distance transport. We performed additional ^{14}C dating by accelerator mass spectrometry of two sites, Skipshelleren and Vistehulen, to clarify the stratigraphy of the sites, as well as material from the previously unpublished site Tjuvanotten (Appendix B). Based on ^{14}C results and stratigraphic information the sites were separated into time periods given in calendar years before present (yr BP): Early Holocene (> 8,000 yr BP), Mid Holocene (c. 8,000 – 4,000 yr BP) and Late Holocene

(c. 4,000 – 1,000 yr BP). The ^{14}C dates were calibrated using CALIB 5.0.1 (Stuiver and Reimer, 1993), based on the data set IntCal04 (Reimer *et al.*, 2004), with 2σ ranges. All dates reported in the text are in calibrated calendar years.

Relative abundance in Skipshelleren

Skipshelleren was excavated in 1930-31 and separated into seven distinctive stratigraphic layers, with transition zones (Bøe, 1934). Seven ^{14}C dates were already available prior to this study (Olsen, 1976; Hjelle *et al.*, 2006), and our new ^{14}C dates (see above) provided at least two dates from each layer. The dates show that layer 1 and 2 cannot be differentiated in time and we consider them as a single unit for this analysis.

The skeletal material from Skipshelleren are highly fragmented, but well preserved, and 23 species of mammals as well as numerous fish and bird species have been identified (Olsen, 1976). The bone material was later revised and the analysis is based on this revision. The site contains 5962 skeletal fragments (including bones, teeth and antler) of moose and red deer that can be traced to a specific layer based on excavation reports. We calculated the total number of identified specimens (NISP) and the relative abundance of moose to red deer NISP in each layer. The change in relative abundance through time was tested using chi-square analysis for linear trend (χ_t^2), as advocated by Cannon (2001). We also calculated the chi-square values (χ^2) of the relative abundance between adjacent layers.

The general morphological similarity between moose and red deer leads us to expect no significant differences in fragmentation or preservation rates. Different butchering and transportation practices (Perkins and Daly, 1968) might however alter the composition of body parts at a site (Lyman, 1985; Grayson, 1989), which can affect a NISP-based analysis (Grayson and Delpech, 1998). Hunters may for example have discarded more of the larger moose bones at the kill site rather than bringing them home, thereby making moose underrepresented at the site, e.g. the Schlepp effect (Perkins and Daly, 1968). We investigated this by grouping specimens into eight different body part groups; phalanges, metapodials, carpals/tarsals, radius/ulna, tibia, “proximal limb bones” (humerus, femur and scapula), “corpus” (ribs, sternum and vertebra) and “head” (antlers, skull and teeth); and performing a chi-square test to see if there were any differences in the body part representation of the species. We also performed a temporal analysis of the relative occurrence of different body parts by pooling the red deer material into two broad time periods, Late Holocene (layers 1-3) and Mid Holocene (layers 4-7). These pooled layers also include skeletal material from transitional zones that could not be attributed to a specific layer, thereby increasing the sample size to 7984 fragments.

Results

Spatiotemporal pattern of moose and red deer finds

Sites with subfossil skeletal remains of red deer predominates in western Norway during the Holocene, however, visual examination of the data indicate that there appears to be a change through time (Figure 1). The skeletal material indicates that moose were more prevalent than red deer in western Norway during the early Holocene, and that red deer became the predominant wild ungulate from the Mid Holocene onwards. This trend is further strengthened in the Late Holocene in the south-western part of the country. Early and Mid Holocene bone finds from coastal areas in north-western and central Norway are generally scarce, making the distribution in this area uncertain before the Late Holocene.

Changes in the relative abundance of moose to red deer in Skipshelleren

In the Skipshelleren bone assemblage, who is dated to c. 7,500 – 1,800 yr BP, moose are found in small numbers compared to red deer throughout the period (Table 1, Figure 2). Red deer, on the other hand, constitute over 60% of all mammal bones in every layer. Moose are present in all layers with a maximum of about 6.5% of cervid bones in the oldest layer. There is a significant decline in the relative abundance of moose to red deer with time ($\chi_t^2 = 36.21$, $P<0.001$). Only two adjacent layers, 3 and 4 ($\chi^2=7.18$, $P<0.01$), and the combined layers 1-3 and 4-7 ($\chi^2=57.02$, $P<0.01$) differ significantly from each other, showing that moose bones became rarer at the site in the Late Holocene.

Both species are represented by bones from all parts of the body and in similar frequencies for most parts (Figure 3a). Moose remains are, however, more dominated by phalanges causing a significant difference in the body part representation of moose and red deer in the assemblage (χ^2=126.08, P<0.001). There is also a significant change in body part representation of red deer between the combined layers 1-3 and 4-7 (χ^2=142.50, P<0.001), caused by a change in the number of phalanges, however the overall distribution is very similar (Figure 3b).

Discussion

Colonization and establishment in western Norway

During the last glacial maximum, most of the Scandinavian Peninsula was covered by large ice caps (i.e. Andersen, 1980), excluding most of the terrestrial fauna. These melted rapidly in the Early Holocene allowing for large scale colonisation by many species. The oldest remains of moose in southern Sweden has been dated to about 13,200 yr BP (Aaris-Sørensen, 2009) while red deer were present from at least 10,600 yr BP (Liljegren and Ekström, 1996). In Norway, the oldest directly dated finds of moose and red deer are bog finds of shed antlers. These confirm the presence of moose in eastern Norway from around 10,300 yr BP (Grøndahl *et al.*, 2010) while the red deer antler, from Viul in the south-east, has been dated to c. 8,500 yr BP (7,690 ± 90 ^{14}C BP (T-2131), Ø. Wiig, UiO Natural History Museum, pers. com.). Their earliest presence in south-eastern Norway is further confirmed by the finding of moose bones at Tørkop dated between 9,000 – 10,000 yr BP (Mikkelsen *et al.*, 1999) and red deer at Saugbruks dated from c. 8,800 – 8,000 yr BP (Hufthammer, 2006), both close to the border of Sweden.

Only three sites have so far been found in western Norway with identified remains of moose and red deer older than 8,000 yr BP (Figure 1a): Sævarhelleren (site 25), Vistehulen (site 27) and Kotedalen (site 9). Sævarhelleren is a newly excavated site, with material dating between c. 9,000 – 7,800 yr BP, and is not yet fully analysed, however, preliminary results show that moose remains are more abundant than red deer at this site (Bergsvik and Hufthammer, 2009). Moose remains are also much more abundant than red deer in Vistehulen, with NISP = 85 and 17 respectively (Degerbøl, 1951). Skeletal material from this site has been dated to between c. 9,000 – 5,000 yr BP (Indrelid, 1978; Appendix B). Previous analyses (Mikkelsen, 1971; Indrelid, 1978) and our new dates show that the stratigraphy at Vistehulen is unreliable and thus we do not know with certainty how the relative abundance change with time. Moose bones were, however, mostly found in the deeper layers and those of red deer in the upper, and we have dated the presumably oldest bone of red deer from this site to 7,569 ± 109 yr BP (Appendix B). The skeletal material from Kotedalen has been dated to between c. 8,500 – 4,700 yr BP and is heavily fragmented and mostly burned (Hufthammer, 1992). Red deer are more abundant than moose at this site, but only 11 fragments have been identified to either of the species from the Early Holocene.

These finds indicate that moose were more abundant than red deer in the Early Holocene and were a more rapid post-glacial colonizer. However, the number of moose need not have been that large as the sites are highly dominated by wild boar (*Sus scrofa*) (Rosvold *et al.*, 2010). The high abundance of a temperate species such as the wild boar also indicates that conditions should have been good for red deer as well. The reason for this apparently slower colonization is uncertain and the material is too scarce to provide a good explanation. It could be argued that this might in part be an effect of different dispersal behaviour, as female moose are more prone to natal dispersal than female red deer (Liberg and Wahlström, 1995; Loe *et al.*, 2009). However, the capacity for rapid dispersal of red deer has been shown by its expansion to large parts of the country during the last century following a historic population decline (Langvatn, 1998). We cannot be certain that red deer were not present in western Norway before our earliest dates, but the presently available information indicate that it was in low numbers compared to moose.

Climatic reconstructions from western Norway show that the Early Holocene was relatively cool and dry followed by a warm and wet Mid Holocene, about 8,000 – 4,000 yr BP, with summer temperatures up to 2°C higher and winter precipitation up to 225% of today (Bjune *et al.*, 2005). Winter temperatures were also higher and the climate seems to have become more oceanic in the Mid Holocene (Giesecke *et al.*, 2008). Warm wet winters are viewed as positive for contemporary red deer populations in western Norway, as most of the precipitation in these years will fall as rain (Mysterud *et al.*, 2001). Several sites are available from the Mid Holocene (Figure 1b), showing a predominance of red deer remains both among and within sites. This warm climate also lead to the broad-leaved forests reaching their maximum density in western Norway (Moe *et al.*, 1996), indicating that this type of vegetation might have been important for the population increase of red deer.

We have no way of knowing the absolute abundance of animals in prehistoric times. However, the lack of moose bones among the many sites containing red deer indicates a low density of moose in western Norway from the Mid-Holocene onwards. Moose were still found in western Norway but, as illustrated by layers 4-7 in Skipshelleren (Figure 2), in low numbers relative to red deer. The same is true for Olsteinhelleren (site 12) which lies just a few meters from Sævarhelleren (see above). This site is dated to between c. 7,600 – 6,800 yr BP and preliminary analyses show that bones of red deer are more frequent than of moose (Bergsvik and Hufthammer, 2009). The takeover of red deer as the dominating ungulate along the west coast in the Mid Holocene is therefore well in agreement with the hypothesis based on climatic adaptations. On the other hand, the Late Holocene pattern of skeletal remains does not fit with this.

Environmental change in the Late Holocene ungulate habitat

By the end of the Mid Holocene the climate of western Norway started getting colder and the period from about 4,000 yr BP is characterised as cooler and drier than the previous period (Bjune *et al.*, 2005). We would therefore expect moose to become relatively more abundant again in western Norway, but this is apparently not the case (Figure 1c, Figure 2). Skipshelleren and Tjuvanotten (site 26) are from then on the only reliable evidence of the presence of moose in south-western Norway, and the relative abundance of moose to red deer at Skipshelleren has even dropped significantly. Tjuvanotten has not yet been formally excavated but bones of both moose and red deer have been found on the cave floor, dating to 1,500 – 1,400 yr BP (Appendix B). The site is situated close to the Scandes Mountains and lies in a valley leading north-west to Skipshelleren, indicating that they may originate from the same population. Apart from these, both moose and red deer appear in sites further north near the coast in central Norway, closer to one of the present day core areas of moose.

There is some evidence, in the Skipshelleren assemblage, that more bones of moose than of red deer were discarded before reaching the site, as phalanges are overrepresented among moose bones and the skeletal part representation of red deer is more even (Figure 3a). This could indicate an underrepresentation of moose in the material. The feet of ungulates are often brought back to the dwelling as they contain strong tendons that are valuable raw material and because phalanges often remain attached to the skin of butchered animals (Perkins and Daly, 1968; Klein, 1989). Rerunning the analysis using only phalanges produces the same pattern of change between layers as in Figure 2. However, the relative abundance of moose in the Mid Holocene layers increase to an average of 8%, creating a larger difference between the Mid and Late Holocene. Thus the drop in relative abundance in the Late Holocene does not seem to be the cause of different body part representation.

Farming and domestic animal husbandry were introduced to Norway about 6,000 yr BP; but was, at least in western Norway, not firmly established before the Late Neolithic c. 4,500 – 4,000 yr BP (Hjelle *et al.*, 2006; Høgestøl and Prøsch-Danielsen, 2006). This coincides with the reduction in the relative abundance of moose to red deer at Skipshelleren (Figure 2) and the otherwise lack of moose bones in western Norway (Figure 1c). One cannot dismiss that this decrease is a result of changes in hunting habits caused by a more sedentary way of life. However, hunting has continued to be an important part of the Norwegian economy up till modern times and the high species richness in the deposits at Skipshelleren shows a continued hunting economy in addition to animal husbandry (Olsen, 1976). As the largest terrestrial game animal, and a significant source of meat and hide, moose would have been a valuable resource even in a farming society and it is more likely that the lack of moose bones in western Norway indicates real changes the fauna.

Although climate is considered a strong factor in shaping the distribution of species, this can be heavily influenced by biotic interactions and dispersal ability (Davis *et al.*, 1998; Gaston, 2009; Van der Putten *et al.*, 2010). No data concerning interactions with predators or parasites and diseases is available for the Holocene. Parasites and diseases has been suggested as a limiting factor for the southern distribution of moose, however this is linked to a warming climate (Murray *et al.*, 2006). Yet, moose might be more susceptible to spread of disease from the introduced livestock (Geist, 1998; Schmölcke and Zachos, 2005). Interspecific competition between moose and red deer cannot be ruled out but present-day knowledge does not consider it to be particularly important (Ahlén, 1965; Rounds, 1982; Mysterud, 2000). On the other hand, Ahlén (1965, 1975) attributed the recent population increase in Scandinavia in large parts to decreasing livestock grazing and changes in forestry practices. Can the new system of human land use established in early agricultural times also be linked to changes in the ungulate community composition in prehistory?

Many pollen diagrams show deforestation and opening of the landscape following agriculture and the colder climate (Kaland, 1986; Bjune, 2005; Hjelle *et al.*, 2006; Høgestøl and Prøsch-Danielsen, 2006; Hjelle *et al.*, 2010). This started earlier and was most pronounced at the outer coast, with the development of the coastal heathlands, but was also obvious further inland. Western Norway was still largely forested but mostly on the steeper hillsides less favourable to agriculture (Hjelle *et al.*, 2006) and the most productive soils were the first to be cultivated (Overland and Hjelle, 2009; Hjelle *et al.*, 2010). Red deer easily make use of steep hillsides and readily adapt to more open terrains (Clutton-Brock *et al.*, 1982) while the more heavily built moose may have been less able to make use of the remaining forest cover. Early animal husbandry practises could also have been positive for red deer as areas were improved for grazing and a certain degree of cattle grazing has been found to facilitate grazing opportunities for red deer (Gordon, 1988; Kuiters *et al.*, 2005). An analysis of ancient DNA from western Norwegian red deer support this, indicating a large population size around 2,000 yr BP with a high genetic diversity (Rosvold *et al.* unpublished results). Continuous livestock grazing does, however, prevent the growth of browse (Speed *et al.*, 2010; Austrheim *et al.*, 2011), and has been found to limit food availability for moose (Wolfe, 1974).

During the Early and Mid Holocene the tree-line altitudes were higher than today and forest covered much of the present-day alpine tundra regions like Hardangervidda (Moe, 1979; Aas and Faarlund, 1988; Bjune, 2005). This would have linked forested habitats on either side of the Scandes Mountains, providing an east-west migration route, and we do indeed find traces of moose in these areas (Figure 1). Due to the post-glacial land rise, colder climate and increased human impact through domestic livestock grazing, the tree-line started decreasing around 4-5,000 years ago leaving previously forested mountain areas open (Gunnarsdóttir, 1996; Bjune, 2005; Eide *et al.*, 2006). These areas were until the beginning of the 20th century AD heavily used by humans, both as pastures for livestock and as hunting grounds for wild reindeer (Blehr, 1973; Indrelid, 1993; Olsson *et al.*, 2000; Austrheim *et al.*, 2011). Narrower dispersal corridors restrict dispersal rates (Travis and Dytham, 1999), and immigration of moose from the east could thus have been prevented. Isolated from the eastern core area, the dwindling western populations would have experienced increased demographic stochasticity and greater risks of local extinction (Stacey and Taper, 1992; Lande *et al.*, 2003).

Agricultural expansion has also been suggested as a cause for the Holocene decline of moose in continental Europe (Schmölcke and Zachos, 2005) and seems a likely explanation for western Norway. The transformation from a forested landscape to a more open cultural landscape also coincided with the loss of wild boar in Norway (Rosvold and Andersen, 2008), indicating that even early agriculture had an influence on the distribution of wild ungulates. Red deer seem to have tackled these changes better. Deforestation was, however, greatly expanded by technological advancement and a growing human population during the last two millennia BP (Rolstad *et al.*, 2001; Myhre, 2004). At the same time genetic analyses indicate that red deer also suffered a decrease in numbers (Rosvold *et al.* unpublished results), leading to restricted and fragmented populations which lasted until the end of the 19th century (Collett, 1909). As an effect of modern forestry and less livestock grazing much land has again become forested and the tree lines are presently rising (Aas and Faarlund, 1995; Hofgaard, 1997; Speed *et al.*, 2010). Strict management of hunting practices have allowed the populations of both moose and red deer to increase considerably during the last decades (Austrheim *et al.*, 2011). Following this, red deer have spread into eastern Norway and moose are again observed in the inner parts of western Norwegian fjords.

Conclusions

The European landscape has a long history of human modifications and faunal exploitation. Even so, the European fauna has retained a distinct biogeographical distribution of species indicating that climate is still one of the main controlling factors (Heikinheimo *et al.*, 2007; Rueda *et al.*, 2010). Direct or indirect effects of future climatic warming are expected to alter the distribution of wild ungulates, increasing the range of temperate species and limiting the distribution of northern species (Mysterud and Sæther, 2011). Our results from western Norway show that the transformation from a forested landscape to a more open cultural landscape produced changes in the fauna contrary to expectations based solely on climate change. This does not mean that future climate change will not affect distribution boundaries, but current changes in land use and forest structure might create patterns of change that at first may seem to contradict these predictions. As much the same land use changes occur in large parts of Europe this should have a wider relevance.

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Tables

Table 1 Numbers of identified specimens (NISP) of moose and red deer by stratigraphic layer at Skipshelleren.

Layer	Moose NISP	Red deer NISP	Age (yr BP)
1&2	39	2443	2,600-1,800
3	2	302	3,900-2,600
4	40	972	5,300-3,900
5	34	568	6,200-5,300
6	63	1452	7,100-6,500
7	3	44	7,500-7,100
Sum	181	5781	

Figures

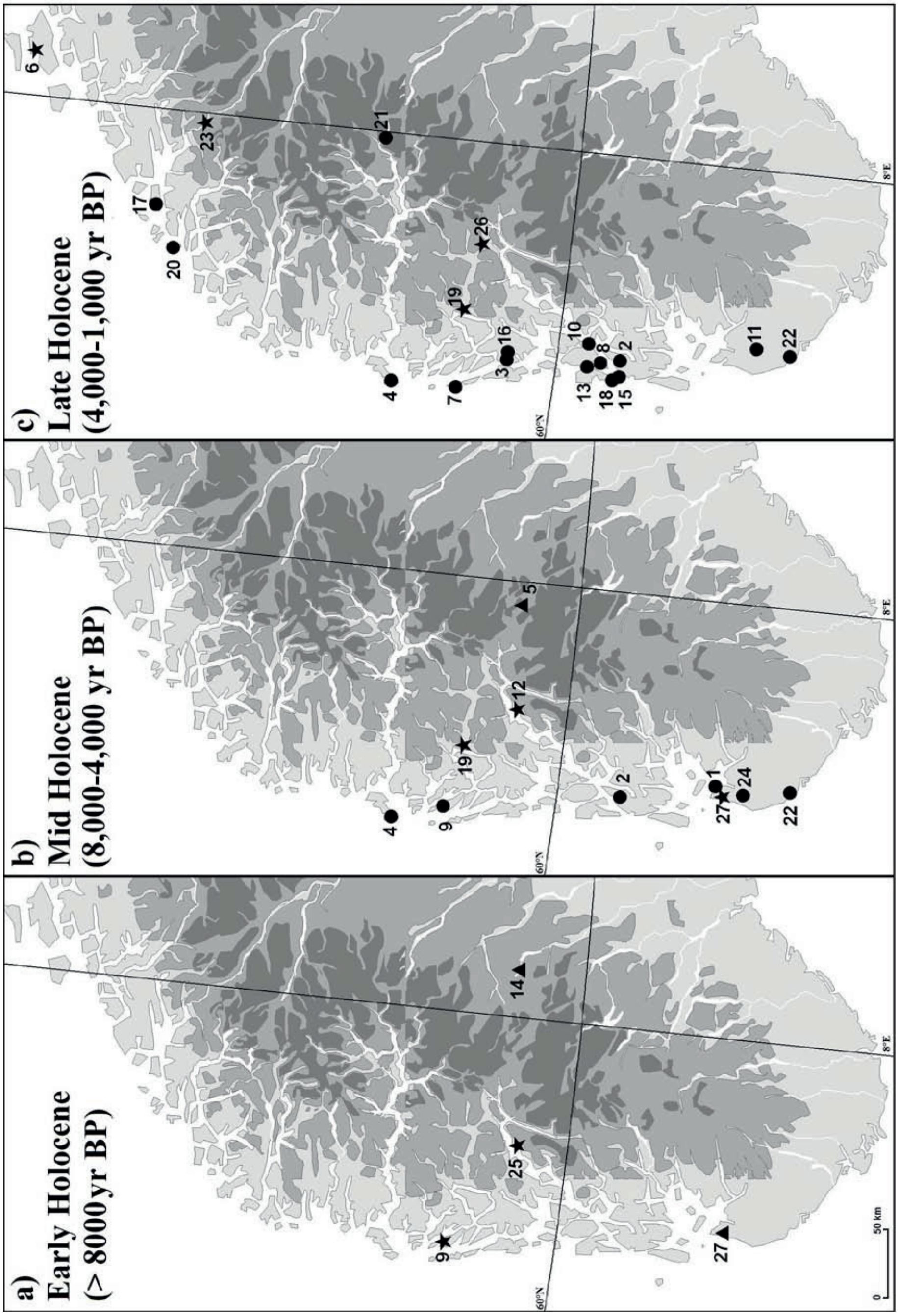

Figure 1 The Holocene distribution of moose (triangles) and red deer (circles) in western Norway and adjacent mountain areas. Sites with remains of both species are marked by stars. More information on the sites are given in Appendix a. Shaded areas represent increasing altitude from light grey (> 600 m.a.s.l) to darkest grey (< 1,200 m.a.s.l). Topographic map modified from Kartverket.

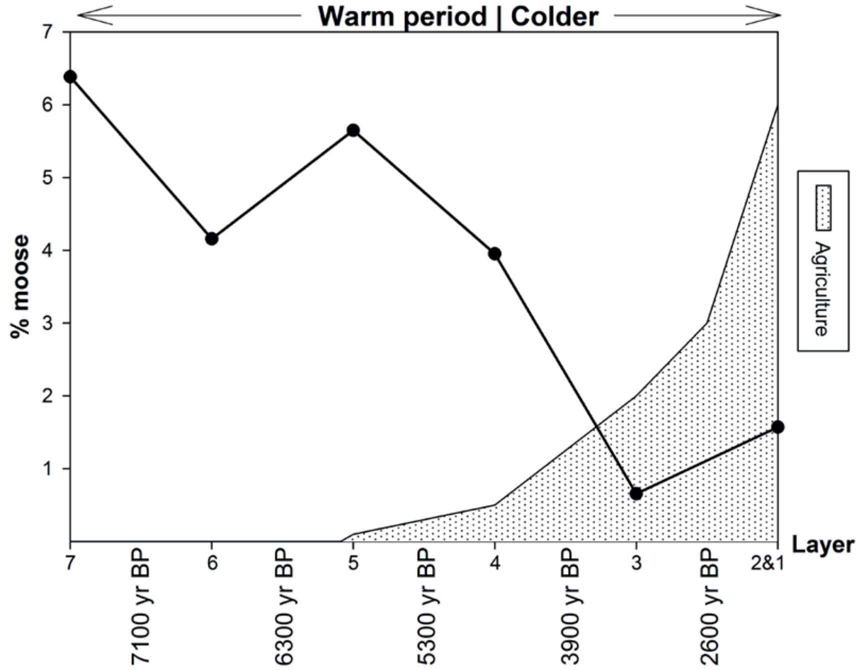

Figure 2 The changing relative abundance of moose to red deer in Skipshelleren. The graph is shown in percentage of moose specimens, according to stratigraphic layer, climate and the increasing farming intensity. Approximate age of layer boundaries are shown in calendar years before present (BP).

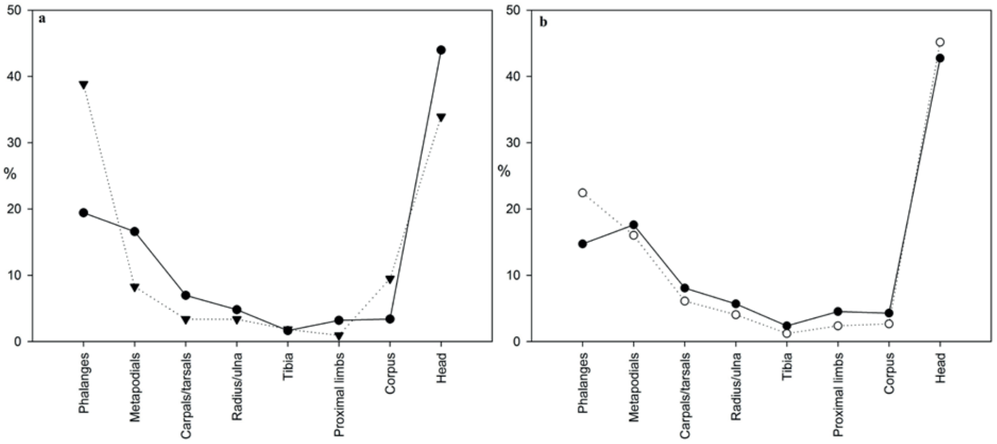

Figure 3 Body part representation at Skipshelleren. a) Total moose (triangles) and red deer (circles) skeletal material. b) Red deer skeletal material at different time periods: Late Holocene (open circles) and Mid Holocene (filled circles).

Appendix

Appendix A

References to the age of sites plotted in Figure 1

	Site	County	Age[1]	Type of date[2]	References to dates
1	Austbø	Rogaland	B	DS	Juhl 2001
2	Geitalemen	Hordaland	B-C	DS, TY	Hougen 1922; Bommen 2009
3	Grimstadneset	Hordaland	C	DB	Rosvold *et al.* (in prep.)
4	Grønehelleren	Sogn og Fjordane	B-C	DS	Jansen 1998; Rosvold *et al.* (in prep.)
5	Halnefjorden	Buskerud	B	DB	Indrelid 1994
6	Hestneshulen	Sør-Trøndelag	C	DB, DS	Petersen 1910; Lie 1991; Rosvold *et al.* 2010
7	Hjartøy	Hordaland	C	DS	Johannesen 1998
8	Kobbehelleren	Hordaland	C	DS	Bommen 2009
9	Kotedalen	Hordaland	A-B	DS	Hufthammer 1992
10	Kuhidlaren	Hordaland	C	DS, TY	Bakka 1972; Bommen 2009
11	Lyngaland	Rogaland	C	TY	Petersen 1936
12	Olsteinhelleren	Hordaland	B	DS	Bergsvik and Hufthammer 2009
13	Osterbakken	Hordaland	C	DS	Bommen 2009
14	Pålsbufjorden	Buskerud	A	DB	Groseth 2004
15	Rundøyno	Hordaland	C	DB	Rosvold *et al.* (in prep.)
16	Ruskeneset	Hordaland	C	TY	Brinkmann and Shetelig 1920
17	Sauehelleren	Møre og Romsdal	C	DS	Nummedal 1913; Rosvold *et al.* 2010
18	Setrehelleren	Hordaland	C	DS, TY	Olsen and Shetelig 1934; Bommen 2009
19	Skipshelleren	Hordaland	B-C	DB, DS	Olsen 1976; Hjelle *et al.* 2006; Appendix B
20	Skjonghelleren	Møre og Romsdal	C	TY	Brøgger 1910
21	Skrivarhelleren	Sogn og Fjordane	C	DS	Prescott 1991
22	Slettabø	Rogaland	B-C	DS	Skjølsvold 1977
23	Smiehelleren	Møre og Romsdal	C	DS	Haug 2012
24	Stangelandshidleren	Rogaland	B	DB, TY	Brøgger 1911; Høgestøl and Prøsch-Danielsen 2006
25	Sævarhelleren	Hordaland	A	DS	Bergsvik and Hufthammer 2009
26	Tjuvanotten	Hordaland	C	DB	Appendix B
27	Vistehulen	Rogaland	A-B	DB	Indrelid 1978; Appendix B

[1] A (>8,000 cal. yr BP), B (8,000-4,000 cal. yr BP), C (4,000-1,000 cal. yr BP)

[2] DB (^{14}C dated bone), DS (^{14}C dated site or layer), TY (typologically dated site)

Appendix B

Results of new radiocarbon dates conducted during this study from three of the archaeological sites

Site	Context	Age in ^{14}C yr BP	Analysed species	Lab. ref.
Skipshelleren	Layer 3	2500 ± 40	*Cervus elaphus*	TUa-5854
Skipshelleren	Layer 5	4655 ± 45	*Alces alces*	TUa-5855
Skipshelleren	Layer 2	2105 ± 40	*Cervus elaphus*	TUa-5856
Skipshelleren	Layer 2	2485 ± 35	*Cervus elaphus*	TUa-5857
Skipshelleren	Layer 7	6275 ± 50	*Cervus elaphus*	TUa-5858
Skipshelleren	Layer 7	6490 ± 50	*Cervus elaphus*	TUa-5859
Skipshelleren	Layer 1	2315 ± 30	*Alces alces*	TUa-5860
Skipshelleren	Layer 1	2070 ± 35	*Cervus elaphus*	TUa-5861
Skipshelleren	Layer 1	2125 ± 40	*Alces alces*	TUa-5862
Skipshelleren	Layer 4	4255 ± 40	*Cervus elaphus*	TUa-6755
Skipshelleren	Layer 1	2790 ± 30	*Sus scrofa*	Poz-25448
Skipshelleren	Layer 1	1875 ± 30	*Sus scrofa*	Poz-25447
Vistehulen	III F:9	7820 ± 50	*Alces alces*	TUa-5944
Vistehulen	IV H:2	7315 ± 60	*Alces alces*	TUa-5945
Vistehulen	X K:3	6405 ± 50	*Alces alces*	TUa-5946
Vistehulen	XIII K:3	7250 ± 45	*Alces alces*	TUa-5947
Vistehulen	IX K:3	6630 ± 45	*Alces alces*	TUa-5948
Vistehulen	IX K:6	6710 ± 70	*Cervus elaphus*	TUa-5949
Vistehulen	XII I:4	7830 ± 60	*Alces alces*	TUa-5950
Vistehulen	XII K:3	8050 ± 60	*Alces alces*	TUa-5951
Vistehulen	XIV K:2	6175 ± 50	*Cervus elaphus*	TUa-5952
Tjuvanotten		1515 ± 40	*Alces alces*	TUa-7758
Tjuvanotten		1535 ± 40	*Alces alces*	TUa-7759

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Paper III

Reconstructing the history of a fragmented and heavily exploited red deer population using ancient and contemporary DNA

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Abstract

Background

Red deer (*Cervus elaphus*) have been an important human resource for millennia. As such, they have experienced intensive human influence through habitat alterations, hunting and translocation of animals. In this study we investigate a time series of ancient and contemporary DNA from Norwegian red deer spanning about 7,000 years. Our main aim is to investigate how increasing agricultural land use and hunting pressure have affected the genetic diversity on a long-term scale. We look for signs of human mediated translocation of foreign animals and investigate the relationship between Norwegian and European populations.

Results

We provide mtDNA (D-loop) sequences from 73 ancient specimens. These samples exhibit a higher genetic diversity than what is found in extant samples, with the highest diversity preceding the onset of agricultural intensification in the Early Iron Age. Using standard diversity indices and Bayesian skyline plot, we detect a population reduction which is more prolonged than but not as severe as historic documents seem to indicate. There are however signs of substantial change in haplotype frequencies primarily due to loss of haplotypes through genetic drift. We provide haplotype networks of western European haplotypes showing two star-like clusters. There is no indication of any human mediated translocations into the Norwegian population. All the Norwegian sequences show a western European origin, from which the Norwegian lineage diverged approximately 15,000 years ago.

Conclusions

Our results provide direct insight into the effects of increasing habitat fragmentation and human hunting pressure on genetic diversity and structure of a population. They also shed light on the northward post-glacial colonisation process of red deer in Europe and highlight the increased precision obtained in studies including both ancient and contemporary DNA when inferring past demographic events.

Keywords

Ancient DNA, habitat fragmentation, harvesting, mitochondrial DNA, genetic diversity, translocation, *Cervus elaphus*

Background

Human populations have a major impact on evolutionary trajectories of other life forms [1-2]. Our activities may modify the genetic diversity and structure of other species through e.g. heavy harvesting, habitat fragmentation and translocation of populations [3-5], often reducing their fitness and future adaptive potential [6-9]. Genetic information may be of importance in order to understand the evolutionary potential and likely responses of populations to past and future environmental changes. However, loss of genetic diversity makes the task of inferring this history difficult. For populations with a complex history several factors can also generate false demographic signals, so that even estimating recent population dynamics might become challenging [10-12].

Red deer (*Cervus elaphus*) has become an important model species for studies of how environmental changes affect large herbivores [e.g. 13, 14]. The species has been present in Europe for at least 400,000 years experiencing several large-scale environmental changes [15-16], and today it is one of the most common and widespread ungulates. However, as an effect of heavy hunting and habitat alterations, red deer were severely reduced in numbers a few hundred years ago. Several populations were driven to extinction or confined to scattered and isolated refugia from which they have later expanded [17]. Even today the widespread distribution is often patchy and fragmented, a trend that is increasing in some areas as a result of habitat loss and overhunting [18], causing reduced local genetic diversity and increased differentiation between areas [19]. Red deer have also been the subject of human mediated translocations of animals, often over large distances, leading to mixing with or substitution of the indigenous population [17, 20-21]. Such translocations, which were often poorly documented, could disrupt long-term local adaptations of populations [22]. Therefore, it is of interest to determine if the patterns and responses to environmental change that we are observing in this model species are caused by genetic drift and adaptation over evolutionary time or if they are the result of recent human interference, like translocation of animals.

Norwegian red deer are among the best studied in the world, and a relatively low genetic diversity has been found in today's populations [23-24]. However, due to a seemingly complex history (see below), relatively little is known with certainty about how they have been affected by the large scale environmental changes and human exploitations during their history [25]. The Norwegian red deer represents the end point of the northward post-glacial colonisation of the western European red deer lineage [26]. Traditionally it has been described as a separate subspecies (*C. e. atlanticus*), but this has not been supported in more recent analyses of skull morphology [27] or molecular systematics [28-29]. The Norwegian deer are, nevertheless, differentiated both morphologically and genetically from the Swedish and Danish populations and seem more closely related to the Scottish deer [23-24, 27, 30]. This differentiation among Scandinavian red deer has been explained either by post-glacial separation and adaptations to different environments, or alternatively, that they originate from different source populations [30-31]. Explanations for the latter hypothesis suggest two waves of post-glacial immigration to northern Europe, with the first wave dominating the Norwegian population, or a translocation of animals by Vikings or in later historic times [23-24, 30, 32]. There are numerous findings of prehistoric red deer bones in Norway and, according to older documents [33-36], they were widespread and numerous in the 16th century AD before rapidly declining in numbers, allegedly as an effect of increased hunting pressure and wolf predation. A similar decline were reported in Sweden [37] and in the 19th century the Scandinavian red deer had been reduced to a few isolated locations, estimated to consist of only a few hundred animals in total [37-39]. Following a period of strict hunting regulations, an almost exponential growth took place during the last century and the current estimated Norwegian census size is well above 100,000 individuals, mainly distributed along the west coast of the Scandes mountain range [32].

In this study we analysed contemporary and ancient genetic diversity in Norwegian red deer in a time-series of mitochondrial DNA (mtDNA) sequences spanning the last 7,000 years. Our aim was to estimate the timing, pattern and magnitude of the historic population decline using different methods to detect past demographic changes. In addition, we explored the relationship to other European populations and the possibility of any human translocation of foreign red deer into Norway. We analysed contemporary DNA together with ancient DNA (aDNA) using Bayesian methods, which is a powerful way to reveal cryptic demographic histories and elucidate genetic effects of bottlenecks [40-43]. As yet there have been relatively few studies using this approach and it is not well known to what extent the inclusion of aDNA by necessity improves the estimation of evolutionary histories using population genetic data. Therefore, we also investigated whether including aDNA significantly changed the outcome of our analyses. Our results provide direct insight into the effects of increasing agricultural land use and human hunting pressure on genetic diversity and structure of a population on a long timescale, and shed light on the northward post-glacial colonization process of red deer in Europe.

Materials and methods

Sampling and dating

To represent the ancient genetic diversity, a total of 142 Holocene samples of subfossil red deer bones, teeth and antlers were collected from nine archaeological sites in Norway for aDNA analysis of the mtDNA control region (D-loop) (Figure 1 and Table 1). Successfully sequenced samples originating from sites which were poorly dated or having an insecure stratigraphy were ^{14}C dated (Table S1 in Additional file 1). ^{14}C dates were calibrated using CALIB 5.0.1 [44] with the calibration curve Incal04 [45] and all dates reported in the text are in calendar years before present (yr BP). The age of the samples range from the Mesolithic to the Late Middle Ages (c. 7,000-500 yr BP) and all samples were collected from the Osteology collections at the University Museum of the University of Bergen.

In order to compare the ancient genetic diversity with extant levels, we compiled data on the contemporary Norwegian mtDNA diversity from previously published literature [29, 46, Haanes et al. unpublished results]. To investigate genetic relatedness between Norwegian and other European populations, as well as investigating the possibility of human-mediated translocations, an extensive list of published haplotypes from extant populations of the western European lineage was also obtained [29, 47-52]. Sequences were downloaded from GenBank and we excluded those from populations described by the authors as being translocated by humans during the last centuries. Sequence lengths varied between the different studies and, in order to compare them to the ancient samples, all were aligned and reduced in size to 327 bp. In addition we provided nine new sequences from contemporary Norwegian animals during primer testing (see below). Information on contemporary sampling is given in Table S2 (Additional file 1).

DNA extraction, amplification and sequencing

We drilled out 30-50 mg of powder from the samples using a Dremel multitool on slow speed. DNA was extracted using Qiagen DNeasy Tissue Kit by adding to the samples 300 µl Buffer ATL, 200 µl 1M EDTA and 35 µl proteinase K, incubating in a thermomixer at 55ºC over night. We used 450 µl of this in extractions following the Qiagen protocol. Polymerase chain reaction (PCR) amplifications of a 327 bp long sequence were performed using two pairs of overlapping primers which were first tested using contemporary samples of red deer:

I: (Ce116F) 5´-CCACCAACCACACAACAAAA-3´ with (Ce343R) 5´-GATCTAGGGGACGGGATACG-3´;

II: (CeCRF251) 5´-TGCCCCATGCATATAAGCATG-3´ with (CeCRR519) 5´-TAGGTGAGATGGCCCTGAAAAAAG-3´.

Amplifications were performed on a GeneAmp PCR System 9700 (Applied Biosystems) in 25 µl reaction mixtures containing 4-8 µl DNA extract, 0.625 U of *PfuTurbo* Hotstart DNA Polymerase (Stratagene), 2.5 µl 10x *Pfu* buffer, 12.5 pmol of each primer, 2.5 µg bovine serum albumin (Sigma) and 200 µM of each dNTP. The PCR profile was 2 min denaturation at 95ºC followed by 46 cycles of 30 s denaturation at 95ºC, 30 s annealing at 72ºC, 60 s of extension at 72ºC, and a final extension step of 10 min at 72ºC. Amplified PCR products were then cleaned using ExoSAP-IT (USB). Sequencing of both strands was performed using BigDye terminator cycle sequencing kit v.1.1 on an ABI 3100 genetic analyser. Sequences were inspected and aligned by eye with aid of MEGA v.4 [53].

Authentication

Several precautions were taken to ensure amplification of authentic DNA from the ancient samples [54-55]. All equipment and working surfaces were cleaned using sodium hypochlorite, ethanol or UV-light. Drilling and extraction were done in designated labs physically separated from post-PCR laboratories, and where no previous work on red deer had been done before. Lab coat and breathing masks were used, gloves were changed frequently and drill bits were changed for each sample. Samples were mechanically cleaned and the outer surface was removed before drilling out the powder. Blank extraction and PCR controls were used in each reaction and only DNA sequences which could be replicated from at least two independent amplifications of each primer pair were used in the subsequent analyses. In addition, the primer pairs were overlapping for 84 bp of the target sequence yielding four replicates or more of the most variable region, thereby ensuring that nuclear copies (NUMTS) could be avoided [56]. We cloned and sequenced a sample of each new haplotype found, using 10 clones from each sample. Cloning was performed according to the Topo TA Cloning protocols (Invitrogen) with PCR-products extracted from gel using the MinElute Gel Extraction Kit protocol (Invitrogen).

Analysing genetic diversity and population structure

A previous analysis using microsatellites found a strong genetic differentiation of the present populations north and south of the Sognefjord area [57]. We therefore pooled our contemporary data into three geographic regions along a north-south transect: the northern part of the distribution, including Møre & Romsdal and Trøndelag counties (N); the Sognefjord area (W); and the southwest, including Rogaland and Hordaland counties (SW). We tested for population structure between the three areas by calculating F-statistics using only haplotype frequencies (F_{ST}) [58] and Φ_{ST} which also accounts for genetic distance between haplotypes [59]. Significance values were obtained after 10,000 permutations using the software Arlequin v. 3.1 [60].

Since most of our samples stem from western Norway and, as some estimates like substitution rate and population size can become biased when analysing populations with a pronounced population structure [61-63], to better satisfy assumptions of panmixia we excluded “site 1” from the ancient samples and the N region from the contemporary data set focusing only on “western Norway” on subsequent analyses of genetic diversity through time, including the Bayesian analyses. The data were divided into four time periods which were treated as separate “populations” in the analyses: c. 7,000-3,500 yr BP (mid-Holocene); c. 2,500-2,000 yr BP (representing the period before any suspected bottleneck and translocations); c. 1,500-500 yr BP (a period including the human Migration Period, the Viking Age and the Middle Ages); and the present.

We calculated standard genetic diversity indices, θ_k [64], Tajima’s D [65] and Fu’s F_s [66] on both the present and ancient data sets using the software Arlequin. θ_k is a measure of haplotype diversity that is sensitive to recent demographic events and should reflect variation in effective population size given a similar mutation rate between populations. Tajima’s D and Fu’s F_s measure departures from equilibrium condition which might be caused by mechanisms such as selection, gene flow or demographic events. Assuming selective neutrality negative, values of Tajima’s D or Fu’s F_s should indicate expansion while positive values indicate population bottleneck.

Bayesian skyline plot

To visualise the change in genetic diversity through time and to explore past demographic changes in the red deer population we used the Bayesian Skyline Plot (BSP) [67] as implemented in BEAST v.1.6.1 [68]. This method allows the inference of the demographic history of a population using a Bayesian approach based on Markov Chain Monte Carlo (MCMC) with the age of the individual sequences as calibrating information for rates and divergence dates [69]. This approach was also used to obtain a direct estimate of substitution rate. Sequence ages were rounded to the nearest 500 yr BP as most samples were not directly dated but were obtained from well dated stratigraphic layers with a certain age range (Table S3 in Additional file 1). Substitution model was selected using the Aikake information criterion in jModelTest v. 0.1.1 [70-71], suggesting the HKY model to best fit the data set [72]. A strict molecular clock was applied and we summarized the lineage coalescent events into ten groups to smooth the estimates over time. MCMC was run for 100 mill iterations, sampling every 10,000th step and with a 10 % burn-in. To estimate model parameters we ran two independent runs which were combined and inspected using TRACER v.1.5 [73]. To evaluate support for the BSP model we also did a run using a constant size coalescent tree prior instead of the BSP, comparing the different runs using Bayes factors [74].

Approximate Bayesian computation analysis

We estimated historical parameters for the Norwegian red deer; i.e. time since immigration(s), effective population size through time, and the genetic effect of bottleneck(s) in modern times; in a coalescence framework using approximate Bayesian computation (ABC) [75] and the DIY-ABC software ver. 1.0.4.37 [76]. Based on the results from the above analyses we explored two different scenarios with either one (scenario 1) or two colonisation events (scenario 2), one being a late translocation event possibly from the British isles during the Viking ages. The two scenarios are depicted in Figure 2.

In two initial runs we compared the effects of using larger effective population size of females than of males (with a ratio of 0.1), compared to a scenario where they were equal, using similar parameter settings and prior ranges as described below. The results did not differ between the two approaches (results not shown), and we therefore did a full scale analysis assuming an equal sex ratio. We modelled two populations: Norway and Europe, with current effective population sizes N_{NOR} and N_{EUR} respectively. To represent the European diversity, one haplotype from 15 different western European populations were randomly picked, 13 from Skog *et al.* [29], one from Nielsen *et al.* [49] and one from McDevitt *et al.* [50]. Such sampling should yield properties approximating those of a random mating population [10, 77-80]. We used the same time periods as described above to represent a serial sampling of the population at four time points (t_0-t_3), with t_0 representing the contemporary sample and t_3 the oldest of the ancient samples (Figure 2). In order to convert time estimates to years instead of generations, we assumed a generation time of four years in female red deer [51]. In scenario 1, the Norwegian population went through a population bottleneck starting at t_{BS} and ending at t_{BE} years back in time, where the effective population size of the Norwegian population is N_{B}. At time t_1, which we allow to occur either within or before the bottleneck period (i.e. we do not *a priori* determine the relative size of t_{BS} and t_1), the Norwegian population is sampled, and prior range for t_1 is set to between 500 and 1,700 yr BP. The sampling at year t_2 and year t_3 is assumed to happen before t_{BS}, i.e., in a period with effective size N_{NOR}, with prior ranges 2,000 – 2,500 yr BP for t_2 and 3,500 – 7,000 yr BP for t_3. In the period between $t_{\mathrm{D}} - x$ and t_{D} the Norwegian population experienced a founder event as a result of the colonisation of Norway, with t_{D} marking the time of divergence from the European population. In scenario 2 we assumed a similar history as in scenario 1, except that there was an immigration and admixture event from the European population before t_{BS} and either before or after the sampling at t_2. The second immigrated population underwent a bottleneck for a total of x years and has an effective size N_{NOR} at the time of admixture. A fraction r of the original Norwegian population and a fraction $1 - r$ of the second immigration contribute to the admixed present day population.

We assumed no migration between populations after divergence, implying that the divergence time estimates are to be treated as minimum estimates. Prior ranges of the effective population size were set to 1,000 – 100,000 for N_{NOR} and N_{B}, and 1,000 – 1,000,000 for N_{EUR}. Based on the results from the Bayesian skyline plot (see below) we assumed that a putative bottleneck started between 500 – 2,500 yr BP and ended 1 – 500 years back in time. The divergence of the Norwegian and European populations was set to occur between 9,000 and 20,000 yr BP. In scenario 2 the second divergence of the Norwegian population from the European occurred between 3,500 and 20,000 yr BP, with an original bottleneck lasting between 1 and 500 years. The admixture between the first and the second Norwegian populations occurred between 500 and 2,500 yr BP, before or after the sampling at t_2.

Mutation rates were treated as nuisance parameters, and we assumed a Kimura 2-parameter model [81] with prior mutation rate estimate range obtained from the BEAST analyses (see below). Summary statistics were computed for each sample in each simulation, i.e. number of haplotypes, Tajima's D, number of private segregating sites and average number of pairwise differences for each pair of populations sampled together. Each scenario was tested using 1 mill simulations, i.e., 2 mill simulations in total for the testing of scenarios 1 and 2.

The scenarios were compared using two approaches; one by directly comparing the summary statistics with the observed diversity in the data set and counting the frequency of the various scenarios among the most similar simulated datasets [82-83], and one by doing a logistic regression of each scenario probability for the most similar simulated data sets on the deviations between simulated and observed summary statistics [84-85]. In the direct comparisons approach the 500 simulated data closest to the observed values were used, while in the regression approach we used 1% of the simulated data closest to the observed data set. Confidence in scenario choice was evaluated by choosing scenario 1 as the true scenario and then simulating 500 data sets using this scenario and parameter values drawn randomly from the prior distributions, and then doing the same for scenario 2. The proportion of times the most likely scenario did not have the highest posterior probability when it was the true scenario was used as an estimate of type I error. The number of times the most likely scenario had the highest probability when it was not the true scenario was used as an estimate of type II error. Parameters were estimated for the most likely scenario using the 1% simulations for a given scenario most similar to the observed data set for the summary statistics employed. In order to evaluate the performance of the estimation procedure, we generated pseudo-observed data sets with known parameter values drawn from the posterior distribution given the most likely scenario. The mean relative bias (MRB), $\frac{1}{n}\sum_{i=1}^{n}\frac{e_i - v_i}{v_i}$, was estimated, where e_i is the i'th estimate of the pseudo-generated true value v, and averaged over the n = 500 data sets.

In order to study the impact of including aDNA samples, we chose the scenario with the highest estimated posterior probability (scenario 1, see below), and re-ran the ABC analyses using only extant DNA samples. In these simulations we assumed a similar history as in scenario 1 above, except that we had no aDNA samples, i.e. $t_1 - t_3$ were not included.

Relationships between haplotypes

Relationships between haplotypes were investigated both on a national and western European level using three different phylogenetic network methods: median-joining in Network v.4.6.0.0 [86], statistical parsimony [87] in TCS v.1.21 [88] and NeighborNet in SplitsTree4 v.4.11.3 [89]. Using network methods instead of standard phylogenetic trees are recommended when working with closely related taxa on a population level as it highlights the uncertainties in the relationships [89-90]. This is also useful when working with reduced DNA fragment sizes, as with aDNA, and using different methods might highlight different areas of uncertainty.

Results

Amplification success and authentication of ancient samples

We successfully sequenced 73 (51.4%) of the ancient samples from which we identified 10 haplotypes: NO1 – NO10 [GenBank:xxx-xxx] (Table S3 in Additional file 1). The success rate was particularly good for the medieval samples from the old towns of Bergen and Trondheim (Table 1). A BLAST search [91] revealed that three of these (NO8 – NO10) had never been described before. None of the negative controls produced red deer DNA, but some samples showed contamination from cattle (*Bos taurus*) when using primer pair II, which is a common problem in aDNA studies [92]. All clones produced identical sequences, except four clones in sample A1348 (NO9) which showed a G-A transition, typical of post-mortem DNA decay [93]. This was only expressed in the clones and was distinct from the segregating site that distinguished this haplotype. Most of the variable sites were also within the overlapping part of the two primer pairs and the independent replicates were always identical. We therefore have good reason to believe that all resulting sequences are authentic.

Present population structure and diversity

All in all we gathered 176 control region sequences (n_N= 86; n_W= 45; n_{SW}=45) from extant Norwegian red deer throughout large parts of its current distribution. From these we identified five different haplotypes (NO1 – NO5), identical to five of the ancient samples. The frequency and distribution of the haplotypes differed strongly among the three regions (Figure 1), with a significant genetic structure (global Φ_{ST}=0.663, $P < 0.001$; global F_{ST}=0.528, $P < 0.001$). Pairwise population differentiation was very high between regions and the most geographically distant populations were also the most genetically differentiated (Table 2). Overall haplotype diversity was moderate in the extant population while nucleotide diversity and θ_k were low, both seemingly lowest in the northernmost area (Table 2). Among the

Tajima's D or Fu's F_s values only the D-value of the Sognefjord population (W) and the combined total genetic diversity of Norwegian deer differed significantly from equilibrium expectations, indicating a recent bottleneck.

Ancient genetic diversity in western Norway

In addition to the five extant haplotypes (four in western Norway) we found five additional haplotypes for the Norwegian population of red deer in the ancient samples. All present day and ancient polymorphic sites are within a 112 bp long central segment of the analysed fragment. The three network methods yielded the same relationship between the ten Norwegian haplotypes showing a close relationship and a star-like pattern with NO4 as the central type (Figure 3). This star-like pattern is not apparent when only considering extant haplotypes. NO4 is also found in the four oldest samples. Among the five haplotypes found in the extant population all but NO3 have been found in samples older than any suspected translocation events. NO3 first appears in two medieval samples from Bergen and Trondheim.

Considering only western Norway from which we have most of our samples it is clear that both the genetic diversity (Table 3) and the relative frequencies of haplotypes (Figure 3) do change to some degree through time. The mid-Holocene samples are highly dominated by the central NO4 haplotype (80% of the samples) which results in fairly low levels of haplotype and nucleotide diversity indices. Samples from this period are more widespread in time, as it spans a period of about 3,500 years. The number of haplotypes increases in the Early Iron Age (about 2,500-2,000 yr BP), with four new haplotypes appearing, and the highest haplotype diversity of all time periods is found in these samples. During the next period (c. 1,500-500 yr BP) diversity is reduced, with only the five haplotypes presently found in the Norwegian populations (NO1-NO5) observed. Further loss of diversity is apparent when proceeding to the present as the once dominant haplotype NO4 is lost in western Norway (W and SW areas) and is only found in the northern area in the present samples. θ_k-values are higher in all the ancient periods compared to the present (Table 3), indicating larger effective female population size in the past. None of the Tajima's D or Fu's F_s values were significant except for the negative F_s value of the mid-Holocene samples (in bold), which remains significant after Bonferroni correction.

Bayesian skyline analysis

The BSP suggest a relatively stable female effective population size, although with a wide confidence interval, until about 2,000 yr BP, when effective size starts to decrease in a stepwise manner (Figure 4). A Bayes factor of 106.8 indicates a strong support for the BSP model over the constant size model, indicating that the BSP reconstruction fits the data better than a constant population size. The estimated substitution rate was 2.78 $\times 10^{-7}$ (95% highest posterior density interval (HPDI): 8.15 $\times 10^{-8}$ – 5.23 $\times 10^{-7}$) substitutions per site per year, which is in line with other studies using aDNA datasets [94-95] and the rate estimated for red deer using only present European diversity [29].

ABC analyses

Both in the direct and logistic approach, scenario 1 in Figure 2 has the highest support (Figure S1 in Additional file 1), i.e. a single colonisation of Norway. The estimated type I and type II error rates are 13% and 21% respectively, implying a statistical power of 79%. The estimated historical parameters based on scenario 1 are presented in Table 4. Median effective sizes of female Norwegian and European populations are N_{NOR} = 7,160 (95% credible interval 1,870 – 32,000) and N_{EUR} = 1.03 mill (95% CI 325,000 – 3.2 mill) and the European and Norwegian populations seemingly diverged from one another t_{D} = 15,280 (95% CI 9,960 – 19,560) years ago. There are only weak signs of bottleneck as modal values of N_B = 10 (95% CI 1,110 – 85,700), but median value being N_B = 22,700, i.e., larger than the N_{NOR} estimate. The larger median value of N_B compared to N_{NOR} is likely an effect of assuming an equal population size before and after the bottleneck. The median time with varying population sizes is $t_{BS} - t_{BE}$ = 976 years (95% CI 452 – 1,704). All time estimates have relatively flat posterior probability distributions and estimates must be interpreted with caution. The bias (MRB) is low (<1) for N_{NOR}, N_{EUR} and N_B effective size estimates and the various time estimates, while moderate for estimated time with possible changes in effective sizes after divergence (x, MRB equals 1.60) (Table 4).

The results from the simulations only using extant samples of DNA, and assuming scenario 1, are shown in parentheses in Table 4. The precision of the estimates are markedly reduced for some of the parameters causing MRB estimates to increase up to 6.8 times for various parameters when excluding aDNA samples compared to estimates including aDNA (average increase in MRB equal to 3.14 across all comparable parameters). However, the parameter estimates have partly overlapping credible intervals and in general the estimates are very similar, except that credible intervals on average is 20% larger in analyses excluding aDNA, i.e., including aDNA is seemingly increasing precision of estimates.

Placement in the western European lineage

We sampled 131 different sequences from the western European lineage which were reduced to 83 different haplotypes after fitting their size to the analysed fragment (Table S2 in Additional file 1). The median-joining and statistical parsimony methods produced similar haplotype networks with the exception of an additional loop in the median-joining (Figure 5). The network shows closely related haplotypes resulting in a large number of cross links. The types cluster in star-like patterns around two central haplotypes identical to NO1 and NO4. The central haplotype is considered to be NO1 by the TCS program. This dual clustering is also apparent in the NeighborNet (Figure S2 in Additional file 1). Five of the Norwegian haplotypes (NO1, NO4 – NO7) are shared with other countries while the other five have so far only been found in Norway.

Discussion

Present day Norwegian red deer populations harbour only a fraction of the haplotype variability present a few thousand years ago, and this can be explained by a moderately severe bottleneck occurring between approximately 1,300 – 300 years ago. Only half of the ancient haplotypes are found in the present population and even less (40%) in western Norway where most ancient samples included in this study have been collected. The larger and more widespread sampling of present deer suggest that the missing haplotypes must be very rare today or have been lost during the historic population decline. Our demographic simulations indicate that this population decline was more prolonged in time but probably not as severe as historic documents seem to indicate. Neither, do we find any indication of human mediated translocation of red deer into Norway.

Reconstructing the demographic history

Red deer colonised western Norway some time before 8,000 yr BP and the high abundance of red deer bones (>60% of all mammal bones) in the deepest layers of Skipshelleren (site 3) indicates that it was well established by the start of the period covered by this analysis (Rosvold *et al*. unpublished results). Around 4,000 yr BP two marked environmental changes started to occur in western Norway. From a warm and wet climate, with temperatures of about 2°C higher than today, the climate became colder and drier [96]. In addition, agriculture was introduced to Norway around 6,000 yr BP but was not properly established in western Norway before around 4,000 yr BP [97]. As red deer is a temperate adapted ungulate, with the Norwegian coast representing the northernmost distribution limit of red deer, it would be fair to predict that such a climate change would affect the population negatively. There is however no indication of this in the BSP (Figure 4) and the significant Fu's F_s indicate population expansion for this period (Table 3). The highly varied topography of western Norway, characterised by many steep-sided and narrow fjords, and their ability to migrate between different altitudes could help buffer against detrimental effects of climatic variations [98], something that the current high density of red deer seems to support [32]. Early agriculture could also have been advantageous for red deer as forest areas were cleared to improve grazing for domestic animals and cattle has, to a certain degree, been found to facilitate grazing opportunities for red deer [99-100]. The Bayesian skyline plot (Figure 4) suggests a relatively stable female effective population size until about 2,000 yr BP with no signal of any expansion. However, as the samples for this early period are widespread in time, the posterior density interval is large and the estimate is thus insecure. The Early Iron Age sample (c. 2,500-2,000 yr BP) has the highest diversity indices of all periods considered (Table 3), indicating that the population size may have been particularly high during this time.

Historical texts tell of a widespread and large population in Norway until around 500 yr BP, after which there was a huge decrease in numbers, allegedly caused by high harvesting rates and increased numbers of predators [33-36], leading to strict hunting regulations [101]. However, as indicated by the diversity indices, the BSP and the ABC analyses, this decrease in genetic diversity appears to have been more prolonged, probably starting before medieval times. The estimated effective population sizes should be interpreted with caution [102-103], but the relative changes can give a reliable picture of the magnitude of the demographic bottleneck. Accordingly, and supported by an earlier study on contemporary microsatellite DNA [24], the bottleneck seems not to have been as dramatic as the historic texts may suggest. The mtDNA diversity in the present population is, however, relatively low (Table 2) and comparable to the Norwegian moose (*Alces alces*) population which has experienced a similar historic population reduction [104], but lower than that found in reindeer (*Rangifer tarandus*) [105]. The lowest red deer mtDNA diversity estimates are found in the northernmost region. We know little of the ancient diversity in this area, but it was described as the area retaining the largest population of red deer after the decline [38] and Tajima's D and Fu's F_S values do not indicate a strong bottleneck (Table 2). However, a lower diversity is as expected in a peripheral population having lost diversity during the colonisation process [106]. The current high population density of red deer in Norway is generally believed to be a recent phenomenon [32], and our results might indicate that at least the effective female population size, as measured through genetic diversity, was higher in the past.

Following the spread of agriculture along the coast, increasingly more forest areas were removed and the once dense coastal forests were transformed into the present day open coastal heathlands [107-108]. From around 2,000 yr BP deforestation were accelerated by human manufacturing of iron, coal, and salt, and later by mining and timber export [109]. This was a time of rapid intensification in agriculture and an establishment of larger farms, leading to a growing human population [110]. The most productive areas were also the ones to be developed first and used by the increasing numbers of humans and domestic animals. These changes in the landscape would have forced the red deer away from optimum habitats, increased habitat fragmentation and possibly reduced migration between areas, thereby isolating populations. Within these fragmented populations there might have been extensive genetic drift, as indicated by the loss of the previously most abundant haplotype (NO4), reducing genetic diversity on a local scale. However, comparing the measured diversity of the entire contemporary Norwegian population (five haplotypes) with the most variable of the ancient samples (seven haplotypes) indicate that overall genetic diversity was not as reduced. Although the Norwegian red deer were severely reduced in numbers and sub-divided, the number of isolated populations were relatively large (at least six) and evenly spread along large parts of its former distribution [38]. Thus, the overall genetic diversity may have been better maintained by the wide geographic spread of the populations than if they had been reduced to a single but larger population [111].

Population fragmentation and isolation is expected to lead to increased genetic differentiation [3], and indeed, there is a high degree of genetic structuring in the present Norwegian female red deer, with the northern population substantially differentiated from other populations (Figure 1 and Table 2). Our estimates based on mtDNA variability are higher than those based on microsatellite markers [57], which could partly be due to the fact that differentiation in mtDNA is expected to be higher than in nuclear DNA due to only half the effective size of the mitochondrial genome. On the other hand, this could also indicate that few females have migrated between the areas since the population size reduction, supporting earlier findings of a pronounced male-biased dispersal tendency of red deer [112-113], and that fjords may act as significant dispersal barriers [57, 114].

Our estimates of population reduction assumes selective neutrality of mtDNA variants, which in some cases might be uncertain [103, 115]. Similar results as ours without implying a population reduction could in certain circumstances be produced through genetic hitchhiking [116]. However, there is no doubt from the historic sources that there has been a reduction in the number of red deer in Norway and qualitatively similar results have been presented from a study of contemporary microsatellite diversity [24].

Colonisation and the western European context

The ten Norwegian haplotypes observed in the ancient samples are closely related to the rest of the western European clade. The star-like structuring (Figure 3) coupled with low nucleotide diversity (Table 3) is indicative of a population expansion from an ancestral haplotype [117] which in this case seems to be NO4. This close relationship coupled with the fact that all present-day haplotypes except NO3 have been found in samples dating to 2,000 yr BP or older is an indication of no human translocation, of at least female red deer, into Norway during historic times. This conclusion is also supported by the ABC analyses, where a scenario of only one post-glacial colonisation of Norway gets the highest statistical support. NO3 is first found at low frequency in late medieval samples and has so far only been found in Norway (Figure 5). A strong genetic drift seems apparent with the loss of the once most common haplotype NO4 from western Norway and it is possible that NO3 originated in Norway and then became frequent in the Sognefjord area (W, Figure 1) as an effect of genetic drift and subsequent population increase during recent times.

An estimated divergence time of the Norwegian population of around 15,000 yr BP (9,960 – 19,560), as indicated by the ABC analysis (Table 4), coincides with the start of the northward colonisation of Europe after the Last Glacial Maximum [26]. The haplotype network for the western European red deer (Figure 5) confirms previous findings of a close relationship within the western European clade [28-29], with little or no apparent geographic structure and several cross-links indicating uncertain relationships. Most of these cross links are between Scottish or Irish samples which have been more extensively sampled [50-51]. Out of the ten haplotypes found in the ancient Norwegian dataset five are shared with other countries. Of these, the two central haplotypes NO1 and NO4 are widespread, being present in Scotland and the border forests between Germany and the Czech Republic [29, 51-52], with NO4 also found in Spain [29], and NO1 being one of the most common types found in the Scottish highlands today [51]. None of the extant Norwegian haplotypes are shared with other Scandinavian countries; although the ancient NO6 is found in Denmark today [49]. The Swedish population seems to have experienced a more severe bottleneck than the Norwegian as only one haplotype, closely related to NO1, is found among indigenous animals [24, 29]. This low diversity makes it hard to postulate the relationship to Swedish animals, but present Scandinavian diversity indicates that some haplotypes never reached Norway and that a large part of those passing through Denmark during the post-glacial colonization (i.e. the Norwegian types) were later lost. Sampling aDNA from both Sweden and Denmark could shed more light on if this was caused by genetic bottlenecks or if they were replaced by later immigrants that never reached Norway.

Two star shaped patterns are apparent among the western European samples, separated by an A-G transition. One of these centres on NO1, which have been described before [29], while the other centres on the closely related NO4 and is made more apparent by our ancient samples. This could be an indication of two subgroups within the western European haplogroup, possibly reflecting different refugial areas in France and Iberia [26]. Most of the European populations have undergone severe population reductions during the last centuries and several translocations which could have distorted any phylogeographic patterns within the haplogroup [17, 118]. However, if we consider these star patterns as different subgroups it becomes apparent that during the Holocene the Norwegian haplotypes centring on NO4 (NO4 – NO10) is gradually replaced by the NO1 subgroup (NO1 – NO3) in western Norway, especially during the apparent population reduction period (Figure 6). It is interesting to note that this does not seem to happen in the northern area. We could interpret this as indicating a second colonisation of red deer in the Late Holocene to western Norway. The ABC analyses do, however, not support this and NO1 have been found among our oldest samples from Norway. A more likely scenario is then of one main immigration event into Norway followed by strong genetic drift during the last two millennia. Strong dispersal barriers, i.e. steep fjords, would have limited northward colonisation and thereby the number of haplotypes spreading far north along the coast.

Conclusions

The emerging picture on the history of red deer in Norway seems more simplified than what some hypotheses would suggest. The ancient DNA indicate that the current genetic diversity and structure can be explained by one immigration event followed by a gradual process of population sub-division and heavy exploitation during the last two millennia, with no sign of any translocation of foreign animals into Norway. It also shows that only females from the western European red deer lineage colonised Scandinavia, supporting previous findings that the eastern lineage had a more limited dispersal into Europe [29, 119]. Apart from a small introduction of German and Hungarian animals to the island Otterøya in the north [46], the Norwegian animals therefore seems to have been free from human induced hybridisation. As the Norwegian red deer seems to be the result of thousands of years of adaptation to the Norwegian landscape and not of human translocations it should be a good model for studying adaptations to environmental change.

The population decline does however seem to have been more prolonged in time than what is told by historic documents, indicating that even early human land use practices had an effect on red deer. Ungulates have been important game animals for humans for a long time and hunting in relation to the agricultural fragmentation of the landscape might have affected the movement and number of animals for a long time, thereby shaping their genetic diversity and structure. These factors should always be considered when studying current responses to environmental changes.

Author's contributions

JR did the laboratory work, analysed the data and drafted the manuscript. HKS performed the ABC-analyses. JR and AKH picked out the ancient samples. KHR supervised the laboratory work. All authors were involved in the study design, revising of the manuscript and read and approved the final manuscript.

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Figures

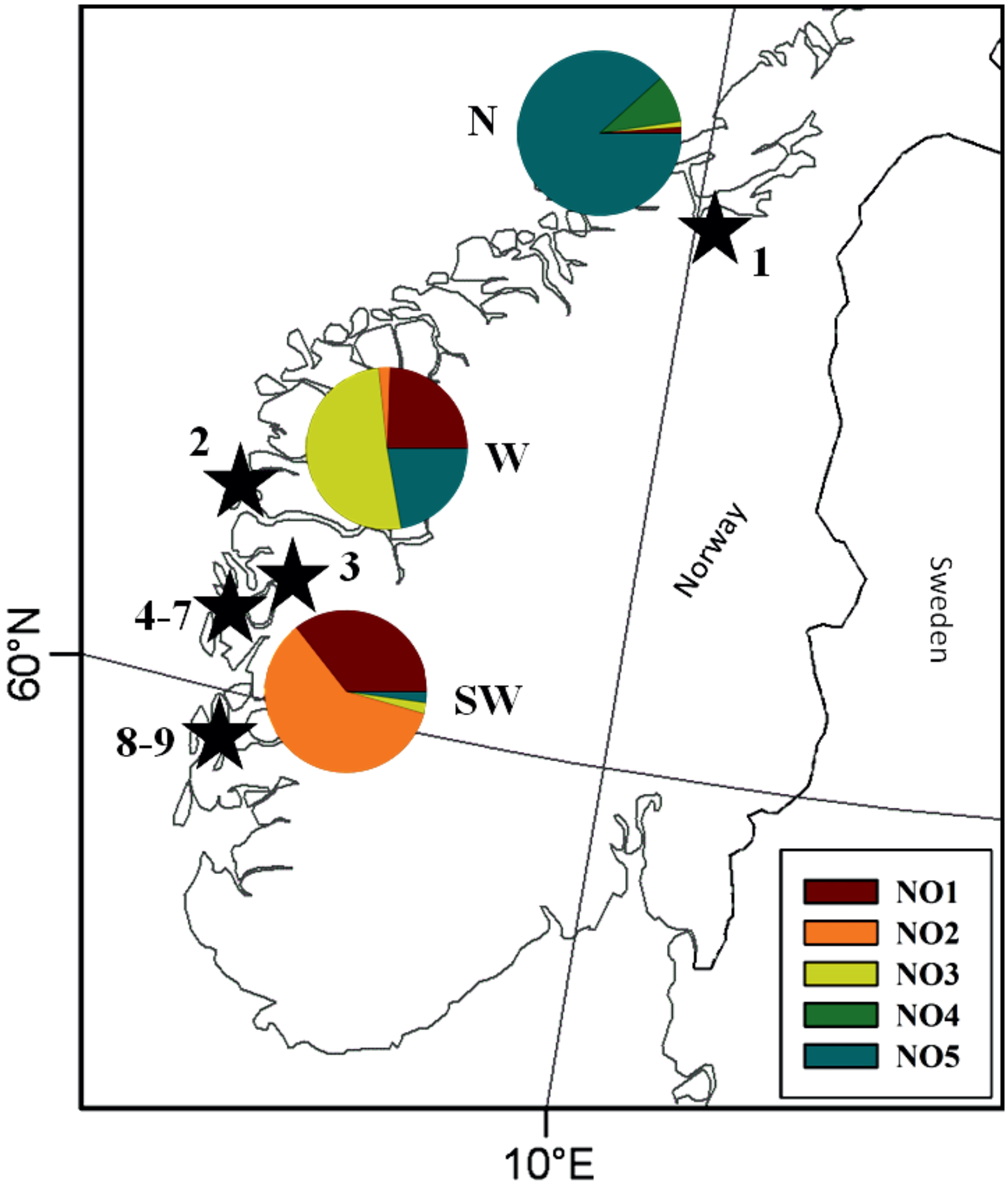

Figure 1 – Study sites and distribution of contemporary red deer mtDNA haplotypes in Norway
Stars mark the distribution of archaeological locations with samples used in the aDNA analyses. 1-Erkebispegården, 2-Grønehelleren, 3-Skipshelleren, 4-Dreggsalmenningen, 5-Rosenkrantzgate, 6-Grimstadneset, 7-Ruskeneset, 8-Rundøyno, 9-Geitalemen. Pie charts show the relative distribution of haplotypes (NO1-NO5) in contemporary red deer in three geographic regions: SW, W and N.

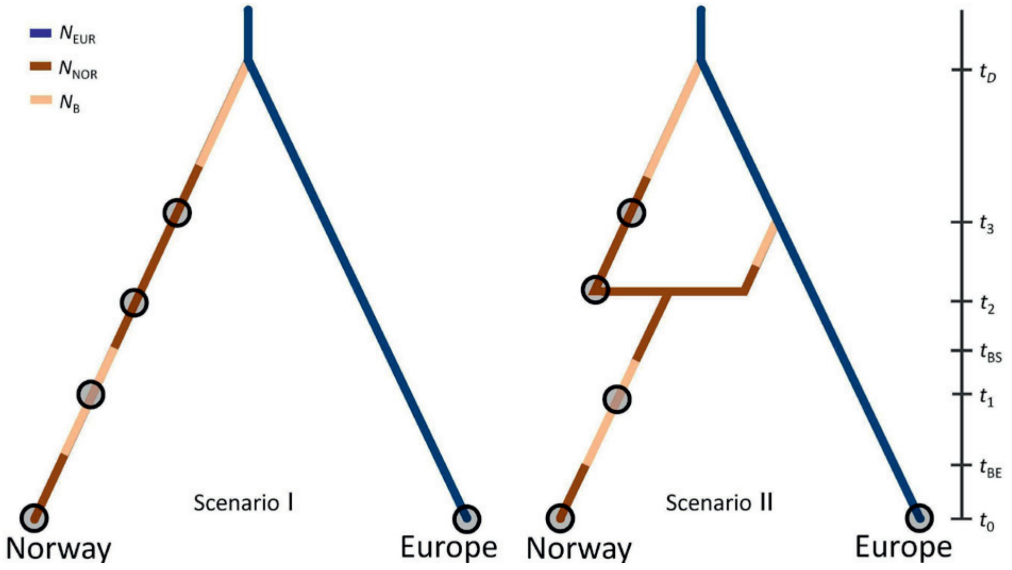

Figure 2 – Overview of the scenarios for the ABC analyses
DNA sampling points are marked by circles. Note that we allow the sampling at t_2 in scenario II to occur either before or after the admixture event.

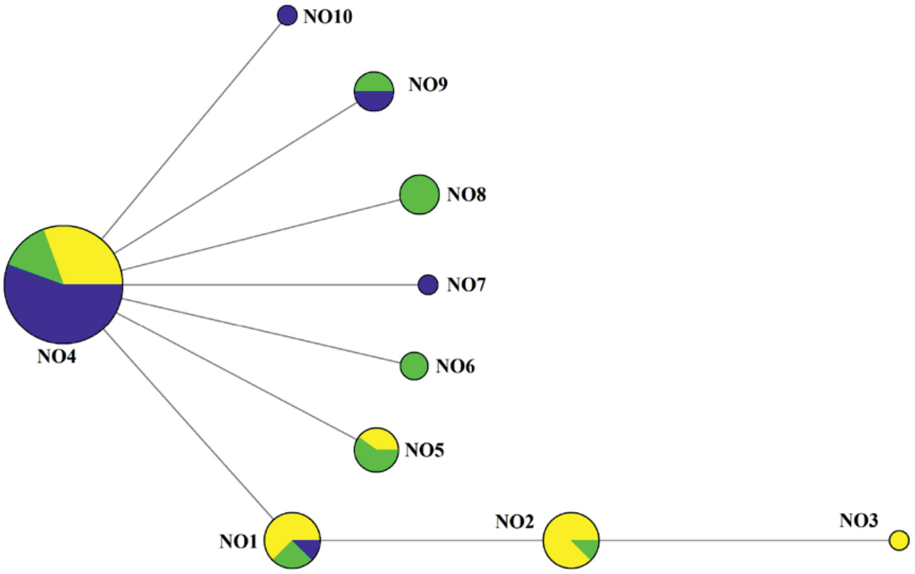

Figure 3 – Haplotype network of ancient Norwegian haplotypes
Size of the circles is scaled according to the frequency of sequences. Yellow: bottleneck period (c. 500-1,500 yr BP), green: pre-bottleneck period (c. 2,000-2,500 yr BP), blue: Mid-Holocene (c. 3,500-7,000 yr BP).

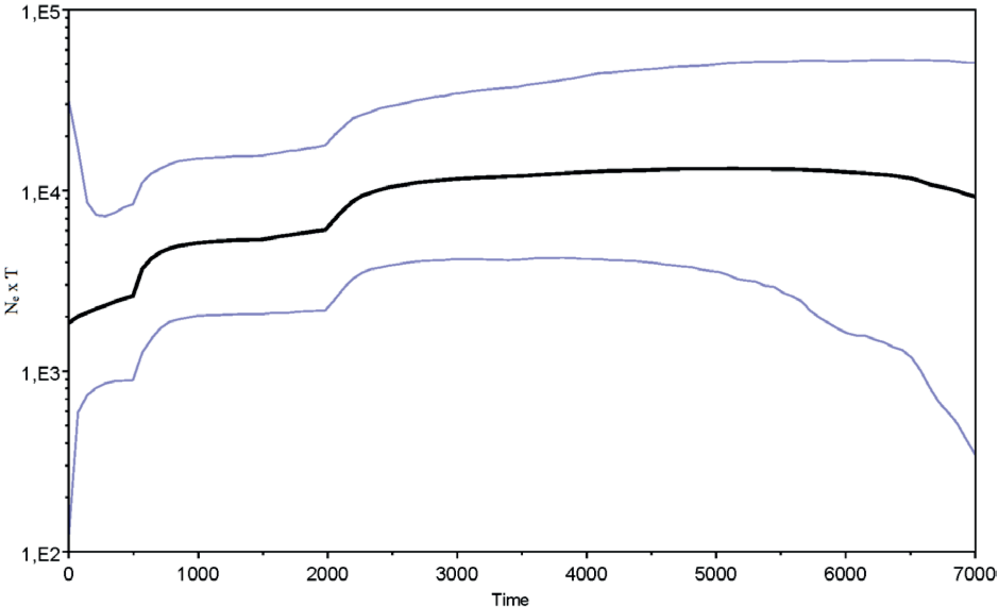

Figure 4 – Effective female population size through time
Bayesian skyline plot (BSP) derived from the ancient and modern red deer dataset of western Norway. The x axis is in calendar years before present and y axis equals changes in effective population size (shown as the product of N_e and generation time T). Black line is the median estimate and the blue lines show the 95% highest posterior density intervals.

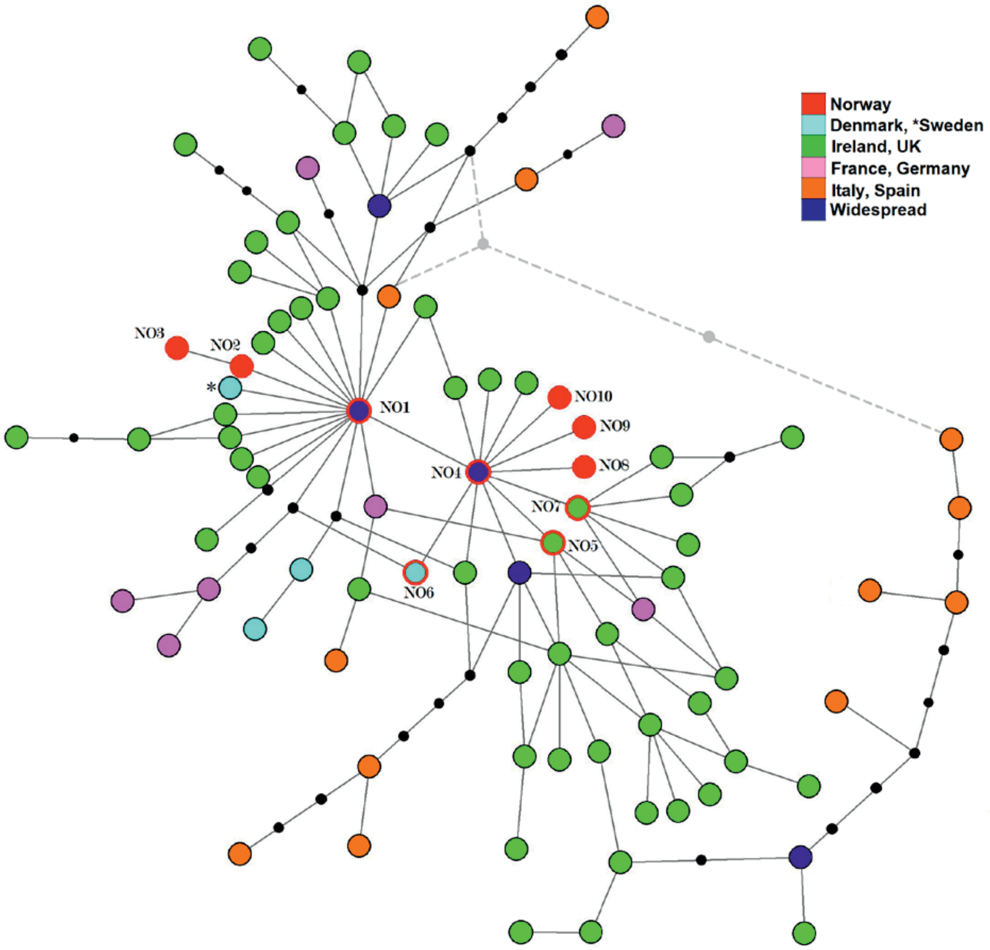

Figure 5 – Relationships between western European red deer
Haplotype network of the western European lineage using both median-joining and statistical parsimony methods. Stapled line show connections only constructed when using the median-joining method. The branch lengths are not scaled to the number of substitutions and missing intermediate haplotypes are shown by black dots. Colour of circles and outlines indicates geographic location. Norwegian haplotypes are marked by named haplotypes. More info on haplotypes can be found in Table S2 in additional file 1.

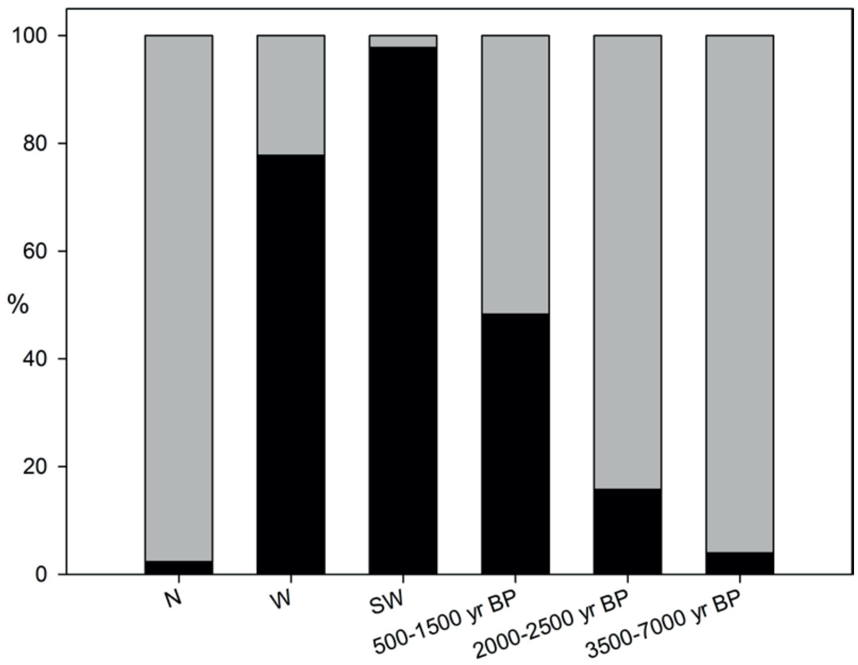

Figure 6 – Change in haplotype frequencies
Proportion of samples with NO1-NO3 (black) versus NO4-NO10 (grey) haplotypes in Norway through time. N, W and SW represent the modern samples in the three geographic regions of current Norwegian red deer distribution.

Tables

Table 1 – Archaeological sites from which samples were taken for aDNA analysis

Table 1 Archaeological sites from which samples were taken for aDNA analysis

Site #	Site name	County	Municipality	c. Age (BP)	# sampl.	Success rate
1	Erkebispegården	Sør-Trøndelag	Trondheim	500	5	60%
2	Grønehelleren	Sogn & Fjordane	Solund	4000-1400	21	48%
3	Skipshelleren	Hordaland	Vaksdal	7500-1800	68	51%
4	Dreggsalmenningen	Hordaland	Bergen	500	2	50%
5	Rosenkrantzgate	Hordaland	Bergen	500	20	95%
6	Grimstadneset	Hordaland	Bergen	2000	7	29%
7	Ruskeneset	Hordaland	Bergen	4000-2000	6	0%
8	Rundøyno	Hordaland	Bømlo	4000-2500	7	29%
9	Geitalemen	Hordaland	Sveio	3800	5	20%

Table 2 - Present mtDNA genetic structure and diversity of red deer for three geographic regions in Norway

Table 2 Present mtDNA genetic structure and diversity of red deer for three geographic regions in Norway

		F-statistics			Genetic diversity indices						
Sample	# seq.	N	W	SW	h	s	H_d	π	θ_k	D	F_s
N	86	-	0.658	0.816	4	4	0.213	0.0009	0.707	-1.268	-1.680
W	45	0.507	-	0.204	4	4	0.643	0.0053	0.861	**2.063**	2.509
SW	45	0.656	0.339	-	4	4	0.524	0.0019	0.861	-0.763	-0.427
Total	176				5	4	0.687	0.0051	0.821	**2.537**	2.979

F-statistics: Φ_{ST} (above) and F_{ST} (below). Genetic diversity indices: number of haplotypes (h) and segregating sites (s), haplotype diversity (H_d), nucleotide diversity (π), theta k (θ_k). Significant values of Tajima's D and Fu's F_s in bold.

Table 3 – Genetic diversity through time in western Norway (W & SW areas)

Table 3 Genetic diversity through time in western Norway (W & SW areas)

Sample	# seq.	h	s	H_d	π	θ_k	D	F_s
Present	90	4	4	0.735	0.0040	0.699	1.368	2.335
Ancient total	70	10	9	0.706	0.0034	2.962	-1.091	-3.756
c. 500-1500 yr BP	26	5	4	0.732	0.0036	1.558	0.355	-0.343
c. 2000-2500 yr BP	19	7	6	0.971	0.0043	3.543	-0.568	-2.420
c. 3500-7000 yr BP	25	5	4	0.363	0.0012	1.509	-1.699	**-3.414**

Notations as in table 2

Table 4 – ABC historical parameter values

Table 4 ABC historical parameter values

Parameter	Median	Mode	$q_{0.05}$	$q_{0.95}$	MRB
N_{NOR}	7160 (13 700)	3450 (7910)	1870 (4590)	32 000 (63 700)	0.11 (0.11)
N_{EUR}	1 030 000 (1 000 000)	684 000 (639 000)	329 000 (325 000)	3 200 000 (2 530 000)	0.21 (0.17)
N_B	22 700 (34 100)	10 (4530)	1110 (2540)	85 700 (92 500)	0.82 (5.17)
x	156 (252)	4 (4)	16 (24)	396 (476)	1.60 (1.61)
t_{BE}	364 (252)	400 (4)	124 (28)	488 (476)	0.33 (2.24)
t_{BS}	1340 (1492)	532 (1360)	576 (600)	2192 (2408)	0.17 (0.18)
t_D	15 280 (15 000)	19 160 (18 520)	9960 (9760)	19 560 (19 560)	0.01 (0.05)
t_1	1120	1268	560	1644	0.12
t_2	2292	2452	2032	2480	<0.01
t_3	4840	3552	3608	6720	0.05

Median, mode, quantiles and mean relative bias (MRB) for the posterior parameters calculated from scenario 1 including or excluding (in parentheses) ancient DNA as estimated from the ABC-analyses.

Additional file 1

Figures

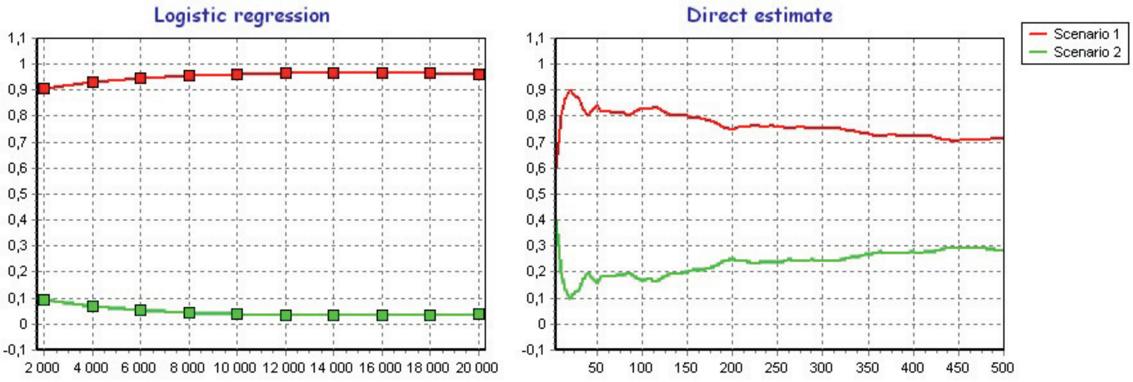

Figure S1 Confidence in scenario choice. Posterior probabilities of the two scenarios using logistic regression and direct comparison approach.

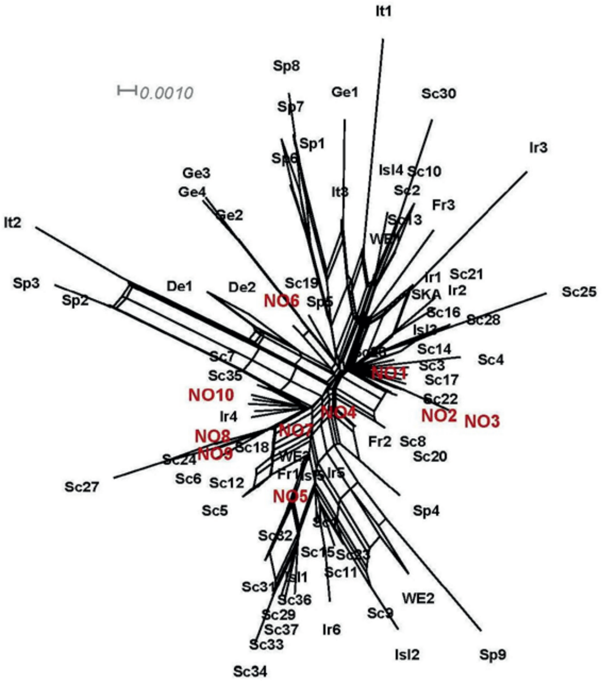

Figure S2 Haplotype network of red deer from the western European lineage constructed using the NeighborNet method implemented in SplitsTree4 v.4.11.3. Norwegian haplotypes highlighted in red. Notations refer to haplotypes in Table S2.

Tables

Table S1 New radiocarbon dates on samples from insecurely dated sites

Sample ID	Site	Age	Lab. ref
1305	Geitalemen	3555 ± 30	TRa-70
1311	Rundøyno	2480 ± 25	TRa-68
1316	Rundøyno	3615 ± 30	TRa-69
1322	Grimstadneset	2040 ± 55	TRa-66
1324	Grimstadneset	1940 ± 30	TRa-67
1332	Grønehelleren	1760 ± 30	TRa-72
1333	Grønehelleren	1650 ± 40	TRa-3066
1335	Grønehelleren	1470 ± 40	TRa-3067
1336	Grønehelleren	4065 ± 45	TRa-3068
1340	Grønehelleren	1560 ± 25	TRa-73
1342	Grønehelleren	1570 ± 40	TRa-3069
1343	Grønehelleren	3080 ± 40	TRa-3070
1344	Grønehelleren	3620 ± 45	TRa-3071
1345	Grønehelleren	1675 ± 40	TRa-3072
1348	Grønehelleren	3120 ± 40	TRa-3073

Table S2 References to red deer haplotypes from the western European lineage used to construct haplotype networks

Haplotype information		Sampling references*							
Haplotype	Countries present	This study	1	2	3	4	5	6	7
NO1	Norway, Scotland, Czech Rep.	NO1	AC1, AD5		H2, H5, H8, H20, H32, H35, H48, H50, H59, H61, H62			HT02	HT10
NO2	Norway	NO2	AC3						
NO3	Norway	NO3	AC4						
NO4	Norway, Scotland, Spain, Germany, Czech Rep.	NO4	AA1, AD6, AD7		H4, H6, H63, H64			HT01	HT8
NO5	Norway, Scotland	NO5	AA7	AF291888	H56				HT7
NO6	Norway, Denmark	NO6				H1, H5			
NO7	Norway, Scotland	NO7			H39				
NO8	Norway	NO8							
NO9	Norway	NO9							
NO10	Norway	NO10							
SKA	Sweden, Denmark		AC2			H3			
De1	Denmark					H6			
De2	Denmark					H7			
Fr1	France		AA8						
Fr2	France		AA9						
Fr3	France		AD2						
Ge1	Germany		AB3						
Ge2	Germany		AC5						
Ge3	Germany		AC6						
Ge4	Germany		AC7						
Isl1	Scotland, Ireland		AD8		H19, H68, H74		MY1		HT9

Isl2	Scotland, Ireland	AD9	H24, H25, H53		NW2	HT6
Isl3	Scotland, Ireland		H1, H3, H15, H29, H40		KNP1, KNP4	HT2
Isl4	Scotland, Ireland, England		H16		NW1	HT4
Isl5	Scotland, Ireland		H65		GY3	
WE1	Denmark, France, Scotland, Ireland	AD1	H9, H60	H2	NW3	
WE2	France, Scotland, Ireland, England	AA3	H18		GY2	HT3
WE3	Spain, Scotland	AA2	H38			
Ir1	Ireland				KNP2, KNP5, KNP7	
Ir2	Ireland				KNP3	
Ir3	Ireland				KNP6	
Ir4	Ireland				GY1	
Ir5	Ireland				GY4	
Ir6	Ireland				WK2	
Sc1	Scotland	AD10	H58			HT13
Sc2	Scotland	AD4	H66			HT11
Sc3	Scotland		H7			
Sc4	Scotland		H10			
Sc5	Scotland		H11			
Sc6	Scotland		H12			
Sc7	Scotland		H13			
Sc8	Scotland		H14			
Sc9	Scotland		H17			
Sc10	Scotland		H21			
Sc11	Scotland		H22			
Sc12	Scotland		H23			
Sc13	Scotland		H26			
Sc14	Scotland		H27			
Sc15	Scotland		H28			
Sc16	Scotland		H30			
Sc17	Scotland		H31			
Sc18	Scotland		H33			
Sc19	Scotland		H34			
Sc20	Scotland		H36, H49			
Sc21	Scotland		H37			
Sc22	Scotland		H41			
Sc23	Scotland		H42			
Sc24	Scotland		H43			
Sc25	Scotland		H44			
Sc26	Scotland		H45			
Sc27	Scotland		H46			
Sc28	Scotland		H47			
Sc29	Scotland		H52			
Sc30	Scotland		H54			
Sc31	Scotland		H55			

Sc32	Scotland			H57	
Sc33	Scotland			H67, H73	
Sc34	Scotland			H69	
Sc35	Scotland			H70	
Sc36	Scotland			H71	
Sc37	Scotland			H72	
Sc38	Scotland				HT5
Sc39	Scotland				HT12
Sp1	Spain		AF291889		
Sp2	Spain	AA4			
Sp3	Spain	AA5			
Sp4	Spain	AA10			
Sp5	Spain	AB1			
Sp6	Spain	AB4			
Sp7	Spain	AB5			
Sp8	Spain	AB6			
Sp9	Spain	AB7			
It1	Italy	AD3	AF291887		
It2	Italy	AA6			
It3	Italy	AB2			

* Haplotype name given by the respective authors

Table S3 Haplotypes of ancient Norwegian samples and modern samples from primer testing, with age used in BEAST analyses and reference to the dating of the site

Sample #	Site	Dating method	BEAST age*	NO Haplotype	Reference
A1194	Skipshelleren	dated layer	2000	4	8
A1197	Skipshelleren	dated layer	2000	5	8
A1199	Skipshelleren	dated layer	2000	4	8
A1201	Skipshelleren	dated layer	2000	4	8
A1202	Skipshelleren	dated layer	2000	9	8
A1208	Skipshelleren	dated layer	2000	8	8
A1209	Skipshelleren	dated layer	2000	6	8
A1211	Skipshelleren	dated layer	2000	8	8
A1212	Skipshelleren	dated layer	2000	8	8
A1213	Skipshelleren	dated layer	2000	8	8
A1214	Skipshelleren	dated layer	2000	5	8
A1215	Skipshelleren	dated layer	2000	1	8
A1216	Skipshelleren	dated layer	2000	4	8
A1218	Skipshelleren	dated layer	2000	9	8
A1222	Skipshelleren	dated layer	2000	6	8
A1223	Skipshelleren	dated layer	2000	1	8
A1229	Skipshelleren	dated layer	5500	4	8
A1236	Skipshelleren	dated layer	6500	4	8
A1237	Skipshelleren	dated layer	6500	4	8
A1238	Skipshelleren	dated layer	7000	4	8
A1239	Skipshelleren	dated layer	4500	4	8
A1292	Erkebispegården	dated site	NA	3	9
A1294	Erkebispegården	dated site	NA	5	9

A1295	Erkebispegården	dated site	NA	5	9
A1296	Dreggsalmenningen	dated site	500	2	10
A1305	Geitalemen	dated sample	4000	4	Supl. 1
A1311	Rundøyno	dated sample	2500	2	Supl. 1
A1316	Rundøyno	dated sample	4000	10	Supl. 1
A1322	Grimstadneset	dated sample	2000	4	Supl. 1
A1324	Grimstadneset	dated sample	2000	5	Supl. 1
A1332	Grønehelleren	dated sample	1500	2	Supl. 1
A1333	Grønehelleren	dated sample	1500	5	Supl. 1
A1335	Grønehelleren	dated sample	1500	2	Supl. 1
A1340	Grønehelleren	dated sample	1500	1	Supl. 1
A1342	Grønehelleren	dated sample	1500	2	Supl. 1
A1343	Grønehelleren	dated sample	3500	9	Supl. 1
A1344	Grønehelleren	dated sample	4000	4	Supl. 1
A1345	Grønehelleren	dated sample	1500	4	Supl. 1
A1346	Grønehelleren	dated layer	3500	4	Supl. 1
A1348	Grønehelleren	dated sample	3500	9	Supl. 1
A1939	Skipshelleren	dated layer	5500	4	8
A1942	Skipshelleren	dated layer	5000	4	8
A1943	Skipshelleren	dated layer	4500	4	8
A1944	Skipshelleren	dated layer	5500	4	8
A1945	Skipshelleren	dated layer	4500	4	8
A1946	Skipshelleren	dated layer	5500	7	8
A1948	Skipshelleren	dated layer	5000	4	8
A1949	Skipshelleren	dated layer	7000	4	8
A1950	Skipshelleren	dated layer	6500	1	8
A1952	Skipshelleren	dated layer	5500	4	8
A1954	Skipshelleren	dated layer	4500	4	8
A1956	Skipshelleren	dated layer	6500	4	8
A1957	Skipshelleren	dated layer	7000	4	8
A1959	Skipshelleren	dated layer	7000	4	8
A2054	Rosenkrantzgate	dated site	500	4	11
A2055	Rosenkrantzgate	dated site	500	4	11
A2056	Rosenkrantzgate	dated site	500	4	11
A2057	Rosenkrantzgate	dated site	500	2	11
A2059	Rosenkrantzgate	dated site	500	4	11
A2060	Rosenkrantzgate	dated site	500	1	11
A2061	Rosenkrantzgate	dated site	500	4	11
A2062	Rosenkrantzgate	dated site	500	3	11
A2063	Rosenkrantzgate	dated site	500	4	11
A2064	Rosenkrantzgate	dated site	500	2	11
A2065	Rosenkrantzgate	dated site	500	4	11
A2066	Rosenkrantzgate	dated site	500	1	11
A2067	Rosenkrantzgate	dated site	500	1	11
A2068	Rosenkrantzgate	dated site	500	5	11
A2069	Rosenkrantzgate	dated site	500	4	11
A2070	Rosenkrantzgate	dated site	500	4	11
A2071	Rosenkrantzgate	dated site	500	2	11
A2072	Rosenkrantzgate	dated site	500	4	11
A2073	Rosenkrantzgate	dated site	500	1	11
M1422	Hitra	contemporary	0	4	
M1690	Mongstad	contemporary	0	1	
M1691	Mongstad	contemporary	0	1	
M1692	Mongstad	contemporary	0	3	

M1693	Mongstad	contemporary	0	1
M1727	Ølve	contemporary	0	2
M1728	Ølve	contemporary	0	1
M1729	Ølve	contemporary	0	2
M1730	Ølve	contemporary	0	2

* Age used in the Bayesian skyline plot analysis

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8: Rosvold, J. (2006). Do single prehistoric dwelling sites reveal changes in the relative abundance of moose to red deer in western Norway? Skipshelleren and the Viste cave. Department of Biology. Trondheim, NTNU. MSc thesis

9: Hufthammer, A. K. (1999). "Utgravningene i Erkebispegården i Trondheim. Kosthold og erverv i Erkebispegården." NIKU Temahefte 17: 1-47

10: Undheim, P. (1985). Osteologisk materiale fra Dreggen: en økologisk studie fra middelalderens Bergen. Bergen Museum. Bergen, University of Bergen. Cand. Philol. Thesis

11: Wiig, Ø. (1981). "Faunal remains from Mediaeval Bergen." Fauna Norvegica Series A 2: 34-40

Paper IV

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987 Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987 Bjørn Åge Tømmerås	Dr. scient. Zoolog	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988 Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988 Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988 Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988 Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989 John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989 Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989 Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989 Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990 Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990 Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990 Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990 Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990 Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990 Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991 Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991 Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991 Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991 Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991 Trond Nordtug	Dr. scient Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods
1991 Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991 Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991 Nina Jonsson	Dr. philos	Aspects of migration and spawning in salmonids
1991 Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992 Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992 Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992 Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992 Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992 Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993 Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993 Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993 Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993 Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993 Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993 Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993 Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993 Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994 Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994 Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994 Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994 Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994 Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994 Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994 Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*

1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors

1997 Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997 Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997 Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997 Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997 Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997 Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997 Trygve Hesthagen	Dr. philos Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997 Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997 Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998 Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998 Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998 Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998 Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998 Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998 Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach
1998 Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999 Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999 Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999 Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999 Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999 Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis

1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems

2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar

2004 Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004 Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004 Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004 Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004 Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004 Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004 Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004 Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005 Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005 Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005 Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005 Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005 Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005 Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005 Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005 Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005 Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005 Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005 Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005 Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005 Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006 Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006 Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006 Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006 Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006 Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006 Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006 Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006 Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006 Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006 Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006 Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006 Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006 P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007 Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007 Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007 Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007 Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007 Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007 Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007 Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007 Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania

2007	Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	ph.d Bilogy	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease

2009	Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments -Focus on formulated diets
2010	Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	ph.d Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	ph.d Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	ph.d Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	ph.d Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	ph.d Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	ph.d Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	ph.d Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	ph.d Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in *Arabidopsis thaliana*

2011	Grethe Robertsen	ph.d Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	ph.d Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	ph.d Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	ph.d Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	ph.d Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	ph.d Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	ph.d Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	ph.d Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	ph.d Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	ph.d Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	ph.d Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	ph.d Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	ph.d Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	ph.d Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	ph.d Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	ph.d Biology	Theoretical and empirical approaches to studying foraging decisions: the past and future of behavioural ecology
2012	Aleksander Handå	ph.d Biology	Cultivation of mussels (*Mytilus edulis):*Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	ph.d Biology	Reproductive and migratory challenges inflicted on migrant brown trour (*Salmo trutta* L) in a heavily modified river
2012	Jisca Huisman	ph.d Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	ph.d Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	ph.d Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	ph.d Biology.	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	ph.d Biology	Optimal performance in the cold

2012	Robert Dominikus Fyumagwa	Dr. Philos.	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	ph.d Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	ph.d Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	ph.d Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	ph.d Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	ph.d Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	ph.d Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*