

Dynamics of large mammal range shifts and extinction: evidence from the Holocene record of Europe

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Author's declaration of originality

I confirm that this thesis is the result of my own work and includes nothing that is the outcome of collaboration or the work of others except where explicitly stated and appropriately referenced within the text and acknowledgements.

Jennifer Crees

June 2013

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“Unfortunately the Holocene fossil record has a somewhat unfashionable reputation among some palaeontologists. This is probably because almost all species studied by Holocene palaeontologists are extant; but also because the time-depth represented by this Epoch is (geologically) tiny and extends in to the present day. However this is in fact this Epoch’s strength; and because the Holocene represents the transition between geological time and ecological time it is in this Epoch that investigations should be prioritised if the aims of palaeontologists are to advance the field of conservation palaeobiology”.

Julien Louys, 2012, *Palaeontology in Ecology and Conservation*, p.258-9.

Abstract

The global extent of past and present biodiversity loss is increasingly well documented, but a focus on investigating timings and correlates of final species extinctions often means that patterns and processes associated with earlier population declines are poorly understood. I used a comprehensive database of zooarchaeological records and regional last occurrence data in order to investigate dynamics of range shift, contraction, expansion and fragmentation of Europe's large mammals over the past 11,500 years, the Holocene Epoch. As a relatively climatically stable period that also witnessed the rapid growth of human populations, it was an ideal model system for studying human impacts on biodiversity over time. Whilst there were inherent biases associated with zooarchaeological data, I was nonetheless able to identify diverse mechanisms of large mammal decline across different species. Despite low numbers of faunal records I was able to attribute the Late Holocene extinction of the European wild ass (*Equus hydruntinus*) to habitat fragmentation associated with postglacial climate-driven vegetation change. Using bootstrapping to control for sampling bias, I then reconstructed temporal and spatial patterns of range contraction across Europe's temperate large mammal fauna from the Mesolithic to the Late Medieval and found that overall, large herbivores experienced significant declines prior to large carnivores. Finally, by combining data from the zooarchaeological, historical and ecological record, I was able to reconstruct through-time patterns of regional extirpation to identify major correlates of species declines as well as calculate species-specific tolerances to human population density. Overall results demonstrate an extinction filter that removed large-bodied species with low tolerance to human impacts from the European landscape from at least the Mid-Holocene onwards. The results from the thesis have relevance across a range of disciplines from palaeontology and zooarchaeology, to ecology and the current day conservation management of large mammals.

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Chapter 1. Introduction

1.1 Large mammal conservation in Europe

Large mammals are recognised as critical components of healthy ecosystems, influencing the structure of plant and animal communities as ‘ecological landscapers’, thus making them a prime focus as both ‘indicator’ and ‘umbrella’ species for conservation (Sinclair 2003). However they are also known to be vulnerable to extinction due to their life history (McKinney 1997; Cardillo *et al.* 2005) and have been disproportionately targeted by humans as prey and/or competitors both in the past (Martin and Klein 1984; Lyons *et al.* 2004) and present (Owen-Smith 1988; Kaul *et al.* 2004). Globally at least one-fifth of all mammals are at risk of extinction in the wild (Hoffman *et al.* 2010) and within Europe nearly one in every six species is threatened with extinction and a further 27% have declining populations (Temple and Terry 2007). Within the large mammal orders Artiodactyla and Carnivora, 21% and 22% of species respectively are threatened with extinction or are extinct (Temple and Terry 2007). Thus despite Europe being one of the best-studied continents in the world, large mammals in this region clearly continue to require conservation attention.

Current global patterns of mammalian species distribution and diversity also belie past anthropogenic influence on the present-day spread of biodiversity and biodiversity threat. Europe currently has lower levels of overall mammalian threat in comparison to tropical regions (Ceballos and Ehrlich 2006; Schipper *et al.* 2008) and large mammals specifically are only at higher risk in tropical regions (Fritz *et al.* 2009). Fritz *et al.* (2009) argued that this phenomenon was probably due to a post-industrial extinction filter that had removed large mammals in temperate regions earlier than in the tropics, citing recent historical declines of carnivores in the region. However Europe’s long history of human and pre-*sapiens* hominin occupation (Roebroeks 2006) potentially provides evidence for an even older pre-industrial extinction filter that has shaped its mammalian faunal assemblage for millennia up to the present day.

1.2 The Holocene

The Holocene is the current geological epoch, dating from the end of the Pleistocene Epoch, about 11,500 years before present (BP), to the present day (Roberts 1998). For the purpose of consistency across the thesis, I also note that subdivisions of the Holocene have now been formally defined as follows: Early-Middle Boundary at 8200 years BP; Middle-Late Holocene Boundary at 4200 years BP (Walker *et al.* 2012). The Holocene is also the Earth’s most recent ‘interglacial’, a climatically warmer period that occurs between longer and colder glacial periods. Such ‘glacial-interglacial’ cycles have characterised the past 2.6 million years of the Earth’s climate, defining the Quaternary Period (Mackay 2009). The most recent glacial-interglacial transition from the Pleistocene to the Holocene also coincided with the final human colonisations of all continents (Goebel *et al.* 2008) and the growth and spread of human populations within these continents facilitated by the ameliorated climate

(McEvedy and Jones 1978; Goudie 2008). Extinctions of large vertebrates that occurred around this climatic boundary have therefore been the subject of vigorous debate regarding climatic versus human causes due to the temporal congruency of these two extinction drivers (e.g. Barnosky *et al.* 2004; Stuart *et al.* 2004; Wroe *et al.* 2006; Nogués-Bravo *et al.* 2008; Pushkina and Raia 2008). Whilst these species are generally collectively referred to as 'megafauna', body size distributions of extinct species varied across continents from 10-1000 kg (Owen-Smith 1999).

By contrast the Holocene period is notable for its relative climatic stability. The climate shifted rapidly from the end of the Pleistocene into the Holocene interglacial period, and temperatures increased in most of Europe (Davis *et al.* 2003). This was interrupted only by the Younger Dryas, a brief cold snap that lasted from approximately 12,900 to 11,600 years BP (Carlson 2010). By about 8000 BP the European vegetation and climate broadly resembled that of the current day (Huntley 1990, Davis *et al.* 2003). Megafaunal extinctions were not the only faunal change during this interval as a result of climatic change; temperate climate biota recolonised northern Europe from southern refugia (Hewitt 1999) combining with species that had survived in cryptic northern refugia (Stewart and Lister 2001). Together, the resultant mammalian assemblage comprised most of the species which we now recognise as biogeographically native in Europe and most of which were widespread across Europe by the Early-Mid Holocene.

The Holocene Epoch has until recently attracted little attention from either ecologists or palaeontologists in terms of extinction research, and has generally been overshadowed by both the preceding end-Pleistocene megafaunal extinctions and the more recent extinction crisis that coincided with the spread of European explorers across the world from around AD 1500 (Turvey 2009b). Yet the Holocene potentially presents a useful model for studying the nature of anthropogenically-mediated extinctions due to the relatively stable climate and increasing human populations during this period (Mackay 2009). Furthermore, because this time period encompasses both recently extinct and extant faunas it could yield important insights into whether large mammals have shown common patterns of response to human pressure over time or whether such responses have been species-specific in nature.

Altogether, there are 255 recorded global mammalian species-level extinctions for the Holocene, only a small proportion of which (if any) can be interpreted as non-anthropogenic events (Turvey 2009c). However, the temporal patterns (extinction chronologies) and processes (causative drivers) vary widely across geographic regions and taxonomic groups and, as relatively little is still understood about the ecological or anthropogenic factors underlying this variation, considerable further research is required. Moreover, the majority of Holocene research has focused on the extinction of insular faunas (e.g. Alcover *et al.* 1998; Simmons 1999; Vigne 1999; Turvey *et al.* 2007), rather than the loss of continental faunas, which has tended to consist of population declines and range contractions of surviving post-Pleistocene faunas rather than complete species extinctions.

This is particularly true of Europe where current-day mammal diversity and threat is low and where only one global extinction, that of aurochs (*Bos primigenius*), has been documented since AD 1500 (Van Vuure 2005). However, if we extend our temporal focus beyond the immediately recent past it becomes apparent that several large-bodied vertebrates became either globally or regionally extinct in the wild during the Holocene in Europe (e.g. Vereshchagin 1959; Spassov 2009; Schnitzler 2011). Many other species are also known to have substantially reduced their geographical ranges from their maximum Holocene extent (Benecke 1999a) to the present day (Mitchell-Jones *et al.* 1999). However, almost no research has been conducted into the timings or drivers of such declines, either at the individual species level or across whole assemblages.

1.3 The zooarchaeological record

The Holocene has a wealth of potential for examining mammalian extinction dynamics due to its extremely extensive and detailed zooarchaeological record. This typically constitutes faunal, usually skeletal, remains that have been accumulated from the excavation of archaeological sites (Reitz and Wing 1999), and which can therefore provide information on spatial and temporal changes in faunal assemblages. This type of evidence is particularly abundant and comprehensive for Europe with its long history of social and natural science research.

Zooarchaeology, or archaeozoology (Bartosiewicz 2001), refers specifically to the study of animal remains from archaeological sites, the aim of which is to gain a better understanding of the relationship between humans and their environment, especially other animal populations (Reitz and Wing 1999). It is very much an interdisciplinary endeavour, incorporating physical, biological, ecological and anthropological perspectives. Basic biological principles that underpin palaeontology also underpin zooarchaeology, thus in theory zooarchaeology can explore faunal change, extinctions and changes in zoogeographical distributions, morphological characteristics, population structure, palaeoenvironmental conditions and relationships between taxa (Reitz and Wing 1999). However, being a fundamentally archaeological discipline it is mostly interested in the relationship between humans and fauna, for example the shift from hunter-gathering to domestication (e.g. Bökönyi *et al.* 1974; Clutton-Brock 1999). In practice, this is also where most research has been focused, i.e. on local, often site-specific, human-related questions. Far rarer has been the use of the zooarchaeological record to research wider macroecological questions where the wild fauna itself is the focus.

Until now, the lack of integrated data on past Holocene mammal distributions at a continental or inter-regional scale has been the main limitation to investigating such large-scale faunal-wide questions, and has resulted in past studies of wild taxa being limited to mostly species- or region-specific case studies (e.g. Van Vuure 2005; Yalden 1999). Archaeologists have noted themselves that the highly scattered nature of zooarchaeological documentation has rendered most of it unexploitable for

researchers in other scientific areas (Audoin-Rouzeau 1993). However, recent acknowledgement of the academic and research benefits of wide-scale databases has led to the compilation of large datasets of European vertebrate records comprising information on species composition, site location and age of bone deposits from archaeological sites (Audoin-Rouzeau 1993; Benecke 1999c; Robert Sommer, Christian-Albrechts-Universität zu Kiel, personal communication, 2008).

Similar databases have already been used to study mammalian spatial distributions over time in the Pleistocene of North America (Graham *et al.* 1996; Lyons 2003). However, spatial studies based on European databases have so far been restricted to descriptive, qualitative reports of zoogeographical distributions (e.g. Markova *et al.* 2001; Sommer and Benecke 2004, 2005a, b, 2006; Sommer *et al.* 2008; Sommer *et al.* 2011). Therefore there is still huge potential for research related to ecology and conservation based on such datasets. For example, it could be used to reconstruct the specific timing and drivers of faunal change in Europe up to the present day, and may also have the potential to provide insight into more general macroecological questions such as the long-term dynamics of species decline, extinction risk and the nature of prehistoric human impacts on past faunas.

1.4 Baselines for conservation research

An understanding of species declines is imperative in the current era of escalating biodiversity loss. As a result, monitoring populations over time has become an integral part of conservation, principally employed in order to detect and predict populations and species in danger of extinction (e.g. Collen *et al.* 2011). Unfortunately monitoring data rarely extends beyond recent decades, which is often inadequate to identify long-term patterns and drivers of decline (Willis *et al.* 2005).

Conservation scientists are increasingly aware of the importance of long-term datasets such as natural history collections for documenting species declines (Shaffer *et al.* 1998; Graham *et al.* 2004). However, to date historical studies have predominantly focused on fisheries (e.g. Patton *et al.* 1998; Jackson *et al.* 2001; Cardinale *et al.* 2009) and marine mammals (e.g. Turvey and Risley 2006; Lotze and Worm 2009) for which intense exploitation during historical periods was well monitored. Conversely, historical harvesting data stretching back more than a few decades for terrestrial populations is harder to come by, meaning that conservationists often lack a reference point for the conservation management of large terrestrial vertebrates. A notable exception is the hunting of North American plains bison (*Bison bison*) by European colonisers from the sixteenth to the nineteenth centuries, with historical accounts suggesting that bison numbered in the many millions prior to widespread targeted hunting (Scott Taylor 2008), and which offers a powerful insight into the potential abundance of large mammal species under low human impact. However in Europe, where much of the large mammal fauna was depleted outside historical memory and its ecosystems have been highly anthropogenically modified (e.g. Benecke 1999a; O'Connor and Sykes 2010), even longer-term data may be required to monitor past mammalian declines.

The question of what constitutes 'long term' in ecology was the subject of a timely letter to the journal *Trends in Ecology and Evolution* (Rull and Vegas-Vallarrubia 2011). Time scales for natural processes can vary enormously depending on the type of scientist being questioned (ecologist, palaeoecologist, palaeontologist etc). However, it is not simply a matter of relativism, but can represent a more fundamental issue regarding ecological baselines and what is perceived as a 'normal' or 'natural' state of biodiversity from which trends and changes should be measured. 'Shifting baseline syndrome' is a well-studied phenomenon in conservation which refers to changing perceptions of biological systems due to loss of experience or knowledge about past conditions (Papworth *et al.* 2008). With regards to conservation, this can mean that extirpations of individuals and populations can seem less severe because the relative loss over time becomes diminished, and the newly impoverished status of an ecosystem becomes the new norm or status quo for the next generation.

Some ecologists have also now acknowledged that past human activity has probably acted as a major extinction filter, and that where species have become extinct soon after human settlement, or just prior to the historical record, such loss has often gone unrecorded (Balmford 1996). The ever-growing list of previously unknown extinct Holocene species (Turvey 2009c) testifies to this fact and provides a note of caution against assessing current biodiversity loss as being a novel human-driven phenomenon.

1.5 Extinction risk

Extinctions, even mass extinctions, are not biologically random, and it is well recognised that certain taxa are more prone to extinction than others (Jablonski 1989; Purvis *et al.* 2000a). A substantial body of literature is focused on understanding the intrinsic and extrinsic correlates of current extinction risk among extant taxa. This is not only of interest to the field of macroecology, but also to conservation science. The ability to identify those taxa that are more prone to extinction can help in turn to predict which species might face particular threat in the future, especially given the likelihood of increasing extrinsic threats. This is vital both to protect the most vulnerable species and also to direct crucial, but limited, conservation resources.

Traits such as high trophic level, large body size, low fecundity, small population and ecological specialisation consistently emerge as biological traits that increase extinction risk, in both modern and fossil extinctions (McKinney 1997; Brook and Bowman 2005). However, most traits, even where common, tend not to be universal risk predictors and will vary between taxa (for example, see Purvis *et al.* 2000b; Johnson 2002; Cardillo 2003). Traits can also be phylogenetically linked, meaning that extinction risk can become highly concentrated within certain taxa: this has potentially severe implications for conservation and today's biodiversity crisis (Heard and Mooers 2000; Purvis *et al.* 2000a). However, an assessment of taxonomic patterns of extinction risk in Holocene mammals

(Turvey and Fritz 2011) found that these differed between past and present, highlighting the potentially distorting effects of historical extinction filters on our perceptions of the relative vulnerability of species. This further underlines the need for longer-term historical and zooarchaeological information on past mammalian losses in order to accurately assess extinction risk in the face of anthropogenic pressures, rather than making assessments based on today's often depauperate mammalian faunas.

Ultimately, the extinction threat that a species or taxon faces arises from the way in which its biology interacts with its environment; in other words, a combination of intrinsic and extrinsic factors. This specific interaction varies across and between ecological groups (Cardillo *et al.* 2008). Cardillo *et al.* (2005) also demonstrated that, whilst extinction risk in smaller species tends to be driven by extrinsic environmental factors, in larger species it is driven by a combination of intrinsic traits and environmental factors. Therefore any research into large mammal extinction must necessarily consider the range of intrinsic and extrinsic factors impacting and shaping a specific species' response to extinction threats.

There are also strong associations between high human population density and persistence of megafaunal species, particularly for carnivores (Woodroffe 2000). However, there is little known about critical thresholds of human impact for either extinct species or for species that have experienced a high degree of historical or prehistoric range loss. How has human impact varied across species, taxonomic groups and geographic areas? Can carnivores persist longer in human-modified habitats than herbivores? Which species are the most vulnerable to human pressures and which are the most resilient? Due to the lack of research carried out at the wider (e.g. guild) level for past populations of extant and extinct species, almost nothing is known of the respective impact of historical and prehistoric human population density on mammal faunas. Past human impact is also of particular interest as this varied across geographical space and intensified over time; this would therefore offer a long term perspective on cumulative human impacts on different species, particularly salient given current estimates of increases in world population (United Nations Population Division 2004).

1.6 Current conservation relevance

Integrating the zooarchaeological record into macroecological research is of more than purely academic interest. Some conservationists have called for the restoration of large mammals to European landscapes following their historical depletion (Taylor 2005). However the concept of so-called 're-wilding' can reflect very different theories and objectives depending on context.

The main proposal refers to restoring populations of extirpated species into their past habitats, whereas 'Pleistocene re-wilding' more controversially proposes populating North American big game parks with Old-World species that are descended from extinct Pleistocene ancestral species or that are ecological proxies for such extinct taxa (Caro 2007). In the context of Europe, re-wilding falls into

two distinct ideas. The more uncontroversial is the use of large grazing herbivores (mostly free-ranging cattle and horses) for habitat management of open grasslands and wetlands. Somewhat more controversial is the movement to release wild populations of recently extirpated native mammals (both herbivores and carnivores) into European landscapes.

In the UK research into the use of free-ranging herbivores for conservation management has been investigated at both the local and national level (Hodder *et al.* 2005). Controlled grazing is now a fairly common method of habitat management on a range of sites across the UK and Europe. It is also seen as an opportunity for controlled and local reintroduction of extirpated and extinct species by way of their domestic counterparts. Heck cattle and Konik ponies have been 'bred back', respectively, from cattle that closely resembled aurochs (Van Vuure 2005) and from the supposedly last wild horses ('tarpan') crossed with Polish domestic horses. These have been released in substantial numbers on some nature reserves in Europe (Wigbels 2001), providing eco-tourism as well as ecological value (Taylor 2005).

The drive to reintroduce ecologically useful megafaunal species to restore landscapes and 'natural' species guilds involves a host of more contentious issues. The drastic alteration of European landscapes due to deforestation and agriculture has left little non-arable productive land that would be suitable habitat for wild mammals, restricting most re-wilding projects to uplands (Taylor 2005). However recent changes in agricultural practice and reductions in yields have potentially opened the way for the release of large areas of farmland for naturalistic grazing (Kirby 2009). Proposals to reintroduce carnivores into landscapes has raised concern for farmers and the public alike, although recolonisations are occurring naturally in many areas as carnivores cross political borders in areas where they are able to expand their range (Trouwborst 2010). These issues are exacerbated by the huge amount of uncertainty over how ecosystems would respond to reintroduced species, partly due to a poor understanding of how guilds of large mammals modified landscapes in the past (e.g. Hodder *et al.* 2009).

Literature on re-wilding has not always been based on sound scientific research into past ecosystems. In reality, knowledge of past Holocene ecosystems remains deeply contested, particularly with regards to their degree of 'openness' and what the 'natural' landscape maintained by grazing megafauna might have looked like (Vera 2000; Birks 2005; Mitchell 2005), most evidence for which comes from pollen records. Faunal communities that existed at the time are also used to infer what the associated ecosystem might have looked like (Vera 2000; Whitehouse and Smith 2004). Yet past abundances of European mammal species, the dynamics of these mammalian communities over time, and the factors associated with the original regional disappearance of species of interest are often still not well understood, thus limiting inferences that can be drawn about the ecosystems in which they persisted and whether or not it is either ecologically or politically appropriate to reintroduce them to landscapes from which they have been lost.

However, if this limited scientific research is to be used as a basis for creating conservation policy and managing landscapes, then knowledge of the 'reference' ecosystem and how it has changed over time is a prerequisite (van Wieren 1995). Furthermore, if extirpated species are to be restored onto or near anthropogenic landscapes, then the reasons for their decline and their response to human presence need to be more clearly understood, in order that potential current-day threats might be mitigated.

This is similarly true for more general reintroductions of species in areas where they have become recently extinct. It is vital to know both the natural distribution of a particular species and its major threats in order to ensure ecologically viable reintroductions. However, reliable information on past distributions and population declines can be limited, even for reasonably well-studied species. During research for this thesis for example, I noted that the IUCN map for the past distribution of European bison (*Bison bonasus*) was incorrect (Pucek 2004), reflecting instead the current consensus on the distribution of the Pleistocene bison of Europe (*B. priscus*). Upon contacting the authors this was acknowledged to be wrong but there appeared to be no intention to rectify this.

Furthermore, there is usually even less information on whether the final areas of persistence of a species even represented the most suitable habitat, and if not, what or where this might be, or have been. Many threatened species exist only in highly fragmented populations in often less than suitable habitat, which alone cannot be used to determine a species' ecology. For example, a report by the IUCN Equid Specialist Group (Moehlman 2002), describing reintroduction potential for the Przewalski's horse (*Equus ferus przewalskii*), stated that 'rating a species' favoured habitat was difficult when the last confirmed observation in the wild was in 1969 [or where a species' distribution is highly fragmented]. Were the remaining individuals in the best habitat available, or in marginal habitat of less interest for other uses by humans?' It has also been proposed that the management of European bison as a forest specialist runs contrary to its evolutionary background and morphology which indicates that it was a characteristic grazer of open, grass-rich habitats, and that its presence in postglacial European forest was as a 'refugee' species in marginal habitat (Kerley *et al.* 2012).

Robust 'baseline' data are therefore crucial for informing conservation management. However, the choice of temporal framework also needs careful consideration as even the use of 'historical' baselines may be insufficient. For example, the great bustard (*Otis tarda*) is the focus of a major conservation reintroduction programme in the UK following documented declines around the sixteenth century and its extirpation in 1832 (Osborne 2005). However, use of zooarchaeological data demonstrated that prior to the Late Medieval period there was no evidence for the species in Britain until as far back as the end-Pleistocene (Yalden and Albarella 2009; Allen 2009). Thus arguably it is not 'native' at all but became extinct following the loss of open landscapes and the postglacial spread of forests throughout Britain in the early Holocene (Yalden 2002). It was probably then introduced into Britain in the Late Medieval for hunting and then was indeed hunted to extinction. The fact that Britain once again has an artificially open (managed) landscape that is a prerequisite for the presence of

great bustard means that it may well now be ecologically suitable; however the current conservation management for this species in the UK is arguably not based on sound scientific evidence, despite the use of 'historical' baselines.

The urgent need for interdisciplinary collaboration between sciences that study both the past and present has been acknowledged (Lyman 1996, 2006; Stahl 1996), but there remains a substantial role for zooarchaeology to be incorporated into conservation research.

1.7 Thesis aims and structure

The Holocene zooarchaeological record is an unparalleled source of information on prehistoric and historical human impacts on mammalian faunas through time. As a long-term dataset that spans both geological and ecological time it does not suffer the limitations of focusing solely on bone assemblages related to extinct species, as with palaeontology, or modern data focused on extant species, as with ecology. An ability to simultaneously study patterns of persistence and decline for both recently extinct and extant species is of unique value in identifying and mitigating ongoing threats to biodiversity. This thesis will therefore investigate the use of the Holocene zooarchaeological record for understanding long-term patterns and drivers of mammalian decline in Europe.

Chapter 2 outlines the general methods and process of data collection that formed the basis for this thesis. This principally included an existing Holocene database of mammalian faunal records for Europe for the past 11,500 years (Benecke 1999a) and additional collection of zooarchaeological faunal records obtained from the literature and visiting institute and museum collections. Chapter 3 investigates possible sources of bias in the European zooarchaeological record. Whilst specific excavation methods are now used to minimise sources of bias in archaeology, when data are pooled into larger datasets, subsequent patterns of intrinsic and extrinsic bias that may arise are rarely acknowledged but can affect the outcome of analyses based on such data. In Chapter 4 I present available data on the Holocene occurrence of the little-known European wild ass (*Equus hydruntinus*) in order to identify the dynamics of its extinction and the possible factors responsible for its eventual demise. As a species that was widespread in the Pleistocene but reduced to remnant fragmented subpopulations during the Holocene, it appears to provide evidence for a temporally non-congruous 'staggered' pattern of megafaunal extinctions in Europe across the Pleistocene-Holocene boundary. Chapter 5 uses the zooarchaeological record for the temperate-adapted Holocene mammalian fauna to analyse spatial and temporal patterns of mammalian species declines from the Early Holocene until the Late Medieval. Due to bias associated with varying sample sizes between species and across time periods, I conclude that raw species occurrence data from the zooarchaeological record is inadequate for reliably reconstructing past species ranges, and therefore employ bootstrapping to identify those species for which significant declines occurred independent of sample size effects. Finally, in Chapter 6 I use ecological, historical and zooarchaeological data to reconstruct last

occurrence patterns for all species across the Holocene to the present day. By combining information on both extinction and survival of species through time I am able to investigate intrinsic and extrinsic correlates of mammal decline. I also use this data to conduct a detailed analysis of thresholds of human population density tolerance for all European large mammal species.

Chapter 2. General methods and data collection

2.1 Introduction

In order to study broad-scale macroecological questions related to dynamics of mammalian ecosystems over time, large quantities of data are required to detect patterns and changes across wide spatial and temporal scales. For the Holocene Epoch the most abundant source of data is the zooarchaeological record: remains of individual bones or bone assemblages from archaeological sites. However, unlike in ecology where systematic presence-absence data can be obtained from careful sampling design, data collected from archaeological sites are obtained opportunistically; in other words the spatial location and date of sites are more or less random. Therefore every effort had to be made to ensure that collection of data included as much of the available material as possible. This chapter describes the process of data collection, protocols for dating and methods for ensuring maximum consistency across the final database.

2.2 Geographic focus

The geographic area covered included all of Europe including Russia up to the Ural mountains, the Caucasus region including Georgia, Armenia and Azerbaijan, and Turkey (fig 2.1). There are many definitions of Europe but this was more or less the fullest in terms of area covered and it also captured the ranges of now regionally extirpated species that lived across parts of Europe during the Holocene. This was considered important in order to fully highlight Europe's past, and therefore arguably its potential, diversity that is now depleted.

As this thesis was focused on continental mammalian assemblages of Europe following the Pleistocene-Holocene transition, the geographical area did include Iceland, as it was not connected to mainland Europe even during the Pleistocene (Ehlers and Gibbard 2004). All Mediterranean islands, except Sicily, were also excluded, as these developed unique insular faunas with characteristic patterns of dwarfing and gigantism, and their evolution and extinction has been well-discussed elsewhere (e.g. Masseti 1998; Simmons 1999; Vigne 1999).

2.3 Focal species

The European large mammal species included in the thesis were defined as those that: i) were native; ii) occupied > 5% Europe's range (based on a species' native Holocene range); and iii) were > 2kg in body mass (Table 2.1). The subsequent assemblage comprised representatives of the orders Artiodactyla, Perissodactyla, Lagomorpha, Carnivora and Rodentia. Due to availability of zooarchaeological data only a subset of these species had sufficient numbers of zooarchaeological records for analysis in Chapters 3 and 5. Four smaller mustelids of interest for which

zooarchaeological data were obtained were also included in these chapters: pine marten (*Martes martes*), beech marten (*Martes foina*), European mink (*Mustela lutreola*) and polecat (*Mustela putorius*). However, last occurrence records were available for a greater number of species through combining zooarchaeological and historical records and so a more complete assemblage of Europe's large mammals was included in Chapter 6.

The postglacial native range of European fallow deer (*Dama dama*) is somewhat unclear. During the Late Glacial its widespread distribution shrank to southern Europe but palaeontological evidence is fragmentary (Masseti 1996). In the early postglacial there was evidence for its presence in southern Italy and the southern Balkans, but in the latter case at least, it was unclear whether this distribution was already human-mediated or not (Masseti 1999) and in general the only part of its current range accepted as harbouring a wild autochthonous population of *D. dama* is Anatolia (Masseti *et al.* 2008). Thus, given the vast extent of anthropogenic intervention in its spread and current range, its native range was conservatively estimated as Turkey only. For this reason, fallow deer was not included in the dataset for Chapter 3 but range maps demonstrating its spread were included within Chapter 5.

Zooarchaeological data for the European wild horse (*Equus ferus*) were not available beyond approximately the mid-Holocene (Sommer *et al.* 2011) as the appearance of domestic horse in the region after this time makes it extremely difficult to identify wild horse remains due to their morphological similarity. Therefore wild horse was also excluded from Chapters 3 and 5. However, the Holocene occurrence of the species was reviewed in a paper included in Appendix 1.

Several species were historically or prehistorically present in regions on the edge of Europe but the size of the area they inhabited was insufficiently large to warrant the species' inclusion in the thesis. These included the now Endangered Persian Fallow Deer (*D. mesopotamica*) formerly distributed in parts of eastern Turkey (Masseti 1996), the now globally extinct Syrian elephant (*Elephas maximus asurus*) that was found in Turkey (Lobban and De Liederkerke 2000) and the regionally extirpated cheetah (*Acinonyx jubatus*) which was present in the Caucasus (Vereshchagin 1959). There was also evidence for Holocene survival in the Urals of the giant deer (*Megaloceros giganteus*) but as this was for the very early Holocene (Stuart *et al.* 2004) and right on the edge of Europe this species was also omitted from the species list.

Taxonomy was based on Wilson and Reeder (2005). Groves and Grubb (2011) recently split red deer (*Cervus elaphus*) into three separate species within Europe: *C. elaphus* (West European red deer); *C. pannoniensis* (East European red deer); and *C. maral* (Turkish/Persian red deer). Genetic analyses have demonstrated large-scale structuring within red deer populations, particularly with regards to eastern and western lineages, that was probably related to glacial refugia (Ludt *et al.* 2004; Skog *et al.* 2011). However, these analyses did not suggest revising the taxonomy of *C. elaphus* and the raising of any subspecies to species level has not been supported or proposed on genetic grounds. Therefore red deer was treated as one species, *C. elaphus*, across Europe for the Holocene period within the thesis.

Groves and Grubb (2011) also split European bison (*Bison bonasus*), into two separate species: *Bos bonasus* (European bison) and *Bos caucasicus* (Caucasian bison). However this was based on morphology alone with no support at the genetic level and they have subsequently been criticised for taxonomic inflation of bovid species (Heller *et al.* 2013). Therefore European bison was also treated as one species, *B. bonasus*, following Wilson and Reeder (2005), across its entire European range in the thesis.

A recent new mitochondrial phylogeny for the Eurasian badger (*Meles meles*) confirmed the existence of four clades, three of which were also supported by morphological data (Del Cerro *et al.* 2010); these were *M. meles*, *M. leucurus* and *M. anakuma*. The suggested range of *M. leucurus* corresponded to the area of Europe east of the Volga River and this was therefore included as a separate species in this thesis. Whilst Del Cerro *et al.* (2010) also recommended that the fourth clade *M. m. canascens*, distributed in south-west Asia (including Turkey and the Caucasus), be raised to species level, this had not yet been accepted as a separate species at the time of writing the thesis (e.g. Kranz *et al.* 2008) and therefore was included here under *M. meles*.

Recent molecular work (Barnett *et al.* 2009) confirmed the existence of three distinct clusters of lion: the extinct Pleistocene cave lion (*Panthera spelaea*), the extinct Pleistocene American lion (*P. atrox*) and the modern lion (*P. leo*). Three geographic clusters have been identified within the modern lion (Barnett *et al.* 2006), of which one, the North African-Asian subgroup, may have recently split into the now-extinct North African Barbary lion (*P. l. leo*) and the Asian lion (*P. l. persica*) (Burger and Hemmer 2006). Whilst it is currently unclear how recently this may have occurred, it is most likely the North African-Asian subgroup that spread into Europe during the Holocene period and which was subsequently extirpated.

Table 2.1 List of species included within each data chapter. Grey denotes availability of data for the species, tick denotes whether the species was included as part of the chapter.

Binomial	Common name	Chapter 3 (Zooarch data)	Chapter 4 (Zooarch data)	Chapter 5 (Zooarch data)	Chapter 6 (Zooarch & historical data)
<i>Alces alces</i> (Linnaeus, 1758)	Eurasian Elk	✓		✓	✓
<i>Alopex lagopus</i> (Linnaeus, 1758)	Arctic Fox				✓
<i>Bison bonasus</i> (Linnaeus, 1758)	European Bison	✓		✓	✓
<i>Bos primigenius</i> Bojanus, 1827	Aurochs	✓		✓	✓
<i>Canis aureus</i> Linnaeus, 1758	Golden Jackal				✓
<i>Canis lupus</i> Linnaeus, 1758	Grey Wolf	✓		✓	✓
<i>Capreolus capreolus</i> (Linnaeus, 1758)	Roe Deer	✓		✓	✓
<i>Castor fiber</i> Linnaeus, 1758	Eurasian Beaver	✓		✓	✓
<i>Cervus elaphus</i> Linnaeus, 1758	Red Deer	✓		✓	✓
<i>Dama dama</i> (Linnaeus, 1758)	Fallow Deer			✓	✓
<i>Equus ferus</i> Boddaert, 1758	Wild Horse				✓
<i>Equus hydruntinus</i> Regalia, 1907	European Wild Ass		✓		✓
<i>Felis silvestris</i> Schreber, 1777	European Wildcat	✓		✓	✓
<i>Gulo gulo</i> (Linnaeus, 1758)	Wolverine	✓		✓	✓
<i>Lepus europeus</i> Pallas, 1778	Brown Hare				✓
<i>Lepus timidus</i> Linnaeus, 1758	Arctic Hare				✓
<i>Lynx lynx</i> (Linnaeus, 1758)	Eurasian Lynx	✓		✓	✓
<i>Lynx pardinus</i> (Temminck, 1827)	Iberian Lynx	✓		✓	✓
<i>Lutra lutra</i> (Linnaeus, 1758)	European Otter				✓
<i>Meles leucurus</i> (Hodgson, 1847)	Asian (Sand) Badger				✓
<i>Meles meles</i> (Linnaeus, 1758)	European Badger				✓
<i>Martes foina</i> (Erxleben, 1777)	Beech Marten	✓		✓	
<i>Martes martes</i> (Linnaeus, 1758)	Pine Marten	✓		✓	
<i>Mustela lutreola</i> (Linnaeus, 1761)	European Mink	✓		✓	
<i>Mustela putorius</i> Linnaeus, 1758	Polecat	✓		✓	
<i>Panthera leo</i> (Linnaeus, 1758)	European Lion	✓		✓	✓
<i>Panthera pardus</i> (Linnaeus, 1758)	European Leopard	✓		✓	✓
<i>Panthera tigris virgata</i> (Illiger, 1815)*	Caspian Tiger				✓
<i>Rangifer tarandus</i> (Linnaeus, 1758)	Reindeer	✓		✓	✓
<i>Saiga tatarica</i> (Linnaeus, 1766)	Saiga Antelope				✓
<i>Sus scrofa</i> Linnaeus, 1758	Wild Boar	✓		✓	✓
<i>Ursus arctos</i> Linnaeus, 1758	Eurasian Brown Bear	✓		✓	✓
<i>Vulpes corsac</i> (Linnaeus, 1768)	Corsac Fox				✓
<i>Vulpes vulpes</i> (Linnaeus, 1758)	Red Fox	✓		✓	✓

*Trinomial specified as it is only the subspecies Caspian Tiger that occupied Europe during the Holocene.

2.4 Zooarchaeological data collection

2.4.1 Zooarchaeological database

The principle data source for all zooarchaeological records was the project “The Holocene History of the European Vertebrate Fauna”. This was a joint cooperation between three German institutions - Deutsches Archäologisches Institut (Berlin), the Institut für Paläoanatomie, Domestikationsforschung und Geschichte der Tiermedizin (Munich) and Institute für Haustierkunde (Kiel). It collected detailed vertebrate faunal remains based on archaeozoological reports from Europe dating from 15,000 BC to the present. The project has been described in a collection of papers edited by Norbert Benecke (Benecke 1999a). The main aims of the project were to amass a reliable and comprehensive framework of faunal data with good spatial and temporal representation to answer the following questions regarding European vertebrate fauna (Benecke 1999c):

- Faunal change at the Pleistocene-Holocene transition
- Formation and evolution of Holocene fauna across Europe
- Distributional changes of postglacial faunas
- Osteomorphological changes in vertebrate species
- Natural and anthropogenic drivers of change in vertebrate faunas

However, to date the database had mostly been used for qualitative regional or species-specific case studies, and had produced no quantitative continent-wide analyses with a specifically ecological focus. Robert Sommer was a post-doctoral researcher working on the project with Norbert Benecke on mammal fauna who agreed to share the database for the purposes of this PhD in 2008. The database provided over 16,000 zooarchaeological records across the focal large mammal species from the Holocene Epoch. It also included a small number of faunal records from natural fossil sites, but these comprised the minority (< 5%). It contained details of the species, the location (country, site, region, latitude and longitude), the date (absolute or relative date) and the reference for the records. All sites included in the database are detailed in Sommer and Benecke (2004).

2.4.2 Additional data collection

Despite being impressively wide-ranging in scope and detail, the authors did note that there was an imbalance in spatial and taxonomic coverage within the database (Benecke 1999c), reflecting the biased nature of the archaeological record, from which the records predominantly originated. Therefore additional data collection was undertaken in order to attempt to balance out some of the uneven coverage and to bring the database as up-to-date as possible.

For example, some species were relatively sparsely populated in the database, such as European bison which had only just over 200 records, in comparison with other large mammals, for example aurochs, which was represented by over 1200 records. To ensure that this was not only an artefact of

sampling, extra sampling effort was concentrated on species low in data. One of Europe's megafaunal mammals, the European wild ass, was also not included in the original database, so data collection was undertaken separately for Holocene records of this species. The data and subsequent analysis for this species are detailed in Chapter 4.

The data provided by Norbert Benecke and Robert Sommer also excluded some European regions, specifically most of former Yugoslavia except Serbia (current day Bosnia and Herzegovina, Croatia, Kosovo, Macedonia (FYROM) and Montenegro) and Albania. This was due to a general lack of zooarchaeological fieldwork in, and therefore data from, the region by the time the database was compiled (Robert Sommer, Christian-Albrechts-Universität zu Kiel, personal communication, 2010). However zooarchaeological fieldwork did gradually resume again in the region around five to ten years ago, and so data collection was undertaken for these countries to attempt to balance out the spatial spread for the whole of Europe.

The definition of Europe in the original database also did not include Turkey and most of the southern Caucasus (Georgia, Armenia, Azerbaijan), so the zooarchaeological literature was intensively searched for Holocene faunal assemblages from these regions. Turkey is a well published region for archaeology and zooarchaeology and 344 faunal records were obtained from 54 sites from published and unpublished literature and personal communication. In contrast, very little has been published in accessible literature for the Caucasus region. The most recent monograph for the whole region was published by N. K. Vereshchagin in 1959. One summary of Georgian Holocene fauna was then published by O. G. Bendukidze in 1979 and one of Armenian Holocene fauna by S. K. Mejlumian in 1988. Nothing similar has been published for Azerbaijan and little has been published in accessible literature for the region apart from Georgia in the last 20 years.

Fieldwork was therefore undertaken in April 2011 to visit museums and institute collections in order to obtain zooarchaeological data from the Caucasus region. Ninna Manaserian from the Institute of Zoology, Armenian National Academy of Sciences, in Yerevan assisted with data collection from Armenia, and Oleg Bendukidze from the Institute of Palaeobiology in Tbilisi assisted with data collection from Georgia. The sources of data included published and unpublished literature, personal communication and museum specimens. Altogether 221 faunal records from 62 sites were collected from Armenia, and 207 faunal records from 36 sites were collected from Georgia. No institution in Azerbaijan responded to requests for either data or to visit collections, but 22 faunal records from 11 sites were obtained from the literature.

Finally, as I obtained the database in 2008, recent publications (from at least the previous five years) were also collected across all species, time periods and European countries where possible, in order that the final database was as up-to-date as possible.

Zooarchaeological records were obtained from published and unpublished literature, grey literature, museum and institute reports, online databases and personal communication. A record was defined as the occurrence of a species within a stratigraphic layer. There could be one or multiple bones from a layer but it was counted as one record so long as this material was stratigraphically related and therefore assigned the same date. Bones found within different dated stratigraphic layers from the same site were counted as separate records. Combining both databases resulted in c.18,670 faunal records across 24 species, with around 85% of the data originating from Norbert Benecke and Robert Sommer's Holocene vertebrate database and around 15% from additional data collection (fig. 2.1). In addition to zooarchaeological records, historical records and other depictions of large mammal species, for example cave paintings and archaeological artefacts, were used to provide further evidence for past species distributions. Due to the inability to formally identify many of these records or to guarantee whether they denoted actual presence of the species in the region, they were not included in analyses; however, they were included in additional maps for interest for species such as lion and leopard whose skeletal remains were rare in the European zooarchaeological record (see Chapter 5).

All extra references that I obtained from data collection are compiled in Appendix 2 of the thesis.

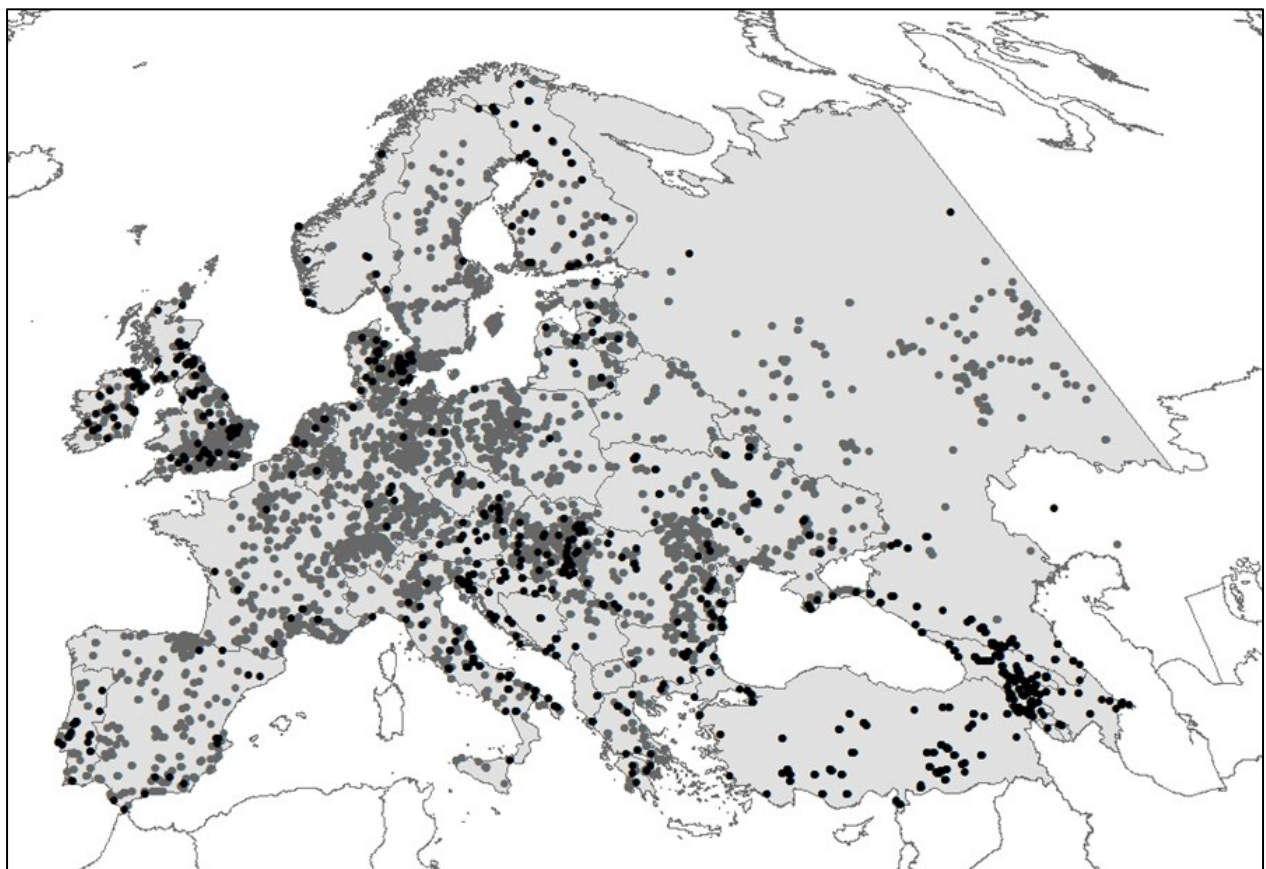


Figure 2.1 Map showing the area of Europe focused on within the thesis (grey shaded area) and zooarchaeological records collected by Jennifer Crees (black circles) and from the Holocene vertebrate database provided by Robert Sommer (grey circles).

2.5 Dating and refining the zooarchaeological database

Using other people's data will invariably result in data that varies in precision and accuracy, and researchers have been found to generate markedly different interpretive conclusions when faced with the same data (Atici *et al.* 2012). As a result there is now increased usage of standardised 'auditing' techniques for dealing with directly and indirectly dated records collected from the literature and other disparate sources, in order to screen them for reliability (Stuart *et al.* 2004; Stuart 2005; Pacher and Stuart 2009; Stuart and Lister 2010). In general, I erred on the side of conservatism with regards to identification and dating of all zooarchaeological records.

In archaeology there are two main methods of dating: i) absolute dating provides an approximate computed date, for example through radiocarbon, thermoluminescence or potassium series dating; ii) relative dating provides an order of events which can be dated in relation to each other, primarily through stratigraphy, where a higher layer may be considered younger than a lower layer which was deposited first. Due to its increased accuracy, absolute dating was preferred over relative dating.

Radiocarbon dating is the main absolute dating technique used to directly date organic remains up to 40,000 years old by measuring levels of the carbon isotope carbon-14 or ^{14}C in a given sample against the natural background level of carbon in the atmosphere (Bowman 1990). These dates are generally reported as uncalibrated, usually a direct number plus a measure of uncertainty; for example 4000 ± 50 BP (Before Present) indicates a standard deviation of 50 radiocarbon years, where the present is defined as 1950. However, because atmospheric levels of radiocarbon in the atmosphere have not remained constant over time, raw calibration dates must be calibrated. Standard calibration curves are available that have measured changes in levels of atmospheric CO_2 over time and several programmes have since been developed that automatically calibrate raw radiocarbon dates. In this thesis all radiocarbon records were calibrated using the calibration curve Intcal 09 in the programme OxCal version 4.1 (Bronk Ramsey 2009) to provide an upper and lower estimate of the date of the faunal sample (in years BC), to around a 95% probability.

Relative dating is generally less precise than absolute dating and can sometimes be erroneous due to complicated stratigraphy that mixes up the usual ordering of layers based on age. However, relative dating is often used in conjunction with absolute techniques, with radiocarbon dating and thermoluminescence used to directly date organic remains and ceramics respectively. This has supported the construction of well-defined chronologies associated with both cultural groups and archaeological time periods.

The following preliminary protocols were first applied to all records across the final zooarchaeological database:

- All zooarchaeological records were mapped in ArcMap 9.3 (ESRI 2008) to cross-check location information from the database and correct assignment of geographic coordinates

(latitude-longitude). Where location information was incorrect, the site or location was searched for in a georeferencing facility such as iTouch (<http://itouchmap.com/latlong.html>) and accurate geographic coordinate information was obtained.

- Where information for records was missing, the original reference was sought and information filled in. If crucial information on the date or location of the record could not be found, it was rejected.
- Where there had been multiple studies on a faunal assemblage or site, the most recent assessment of the data was used.
- Poorly dated records, or records with questionable dates, were rejected.
- Where multiple dates for a site or record were available, absolute dates were preferred over relative dates.
- Where several absolute dates were provided for a site, the most ancient was used for association with a record, in order to be conservative with regards to extinction chronologies and interpreting changes in faunal assemblages over time.
- Where sites or specimens had been re-dated, the most recent dates were used, on the assumption that theory and techniques of assessing archaeological remains have improved over time.
- All radiocarbon records where the raw radiocarbon date was cited were re-calibrated using OxCal for consistency in absolute dating across the database.
- Records older than 10,000 (cal.) BC were not used, due to possible Late Pleistocene age of the material.
- Relatively dated records which spanned more than two archaeological time periods were rejected due to lack of precision.

All final records were then identified as being dated within one of five approximate categories:

Category	Dating of record	Number of records
1.	Radiocarbon (^{14}C) dated	546
2.	Pre-assigned date from original reference related to cultural or archaeological period	7861
3.	Assigned to a culture (e.g. Karanovo I; La Tène)	5123
4.	Assigned to part of an archaeological period (e.g. Early Mesolithic, Middle Bronze Age; Late Iron Age)	2106
5.	Assigned to an entire archaeological period (e.g. Mesolithic, Neolithic, Bronze Age)	3034

No dating method in archaeology can return a single exact date. Even radiocarbon dating can only produce a date interval (following calibration) that is an estimate of the last few years of the animal's life, to within around 95% accuracy. Furthermore, relative dates could not easily be used alongside direct dates without being assigned a numerical time as archaeological periods, for example, were temporally non-congruent across much of Europe due to a lag in diffusions in technology and subsistence methods (e.g. Pinhasi *et al.* 2005). Thus it was most sensible to treat all records within the database as estimated interval dates. Firstly, a dataset was compiled of all cultural periods mentioned in the zooarchaeological database and the dates corresponding to these cultures were searched for and identified, where possible from peer-reviewed sources and also cross-referenced with more than one source. Secondly, a similar dataset was compiled for all archaeological periods mentioned in the database at the country scale for increased accuracy and to encompass the staggered dates across different parts of Europe for these periods (see Appendix 3). In order to be consistent this was compiled mostly from the British Museum's World Timelines website (2010) and James (2005) and for the Caucasus region from the Project ArAGATS website run by Cornell University and the Institute of Archaeology and Ethnography, NAS, Armenia (2010). All dates were converted to years BC/AD, although the majority were collected in this format already. These dates were then transferred back to all relevant records in the original database. Possible biases associated with dating of zooarchaeological remains were addressed in Chapter 3.

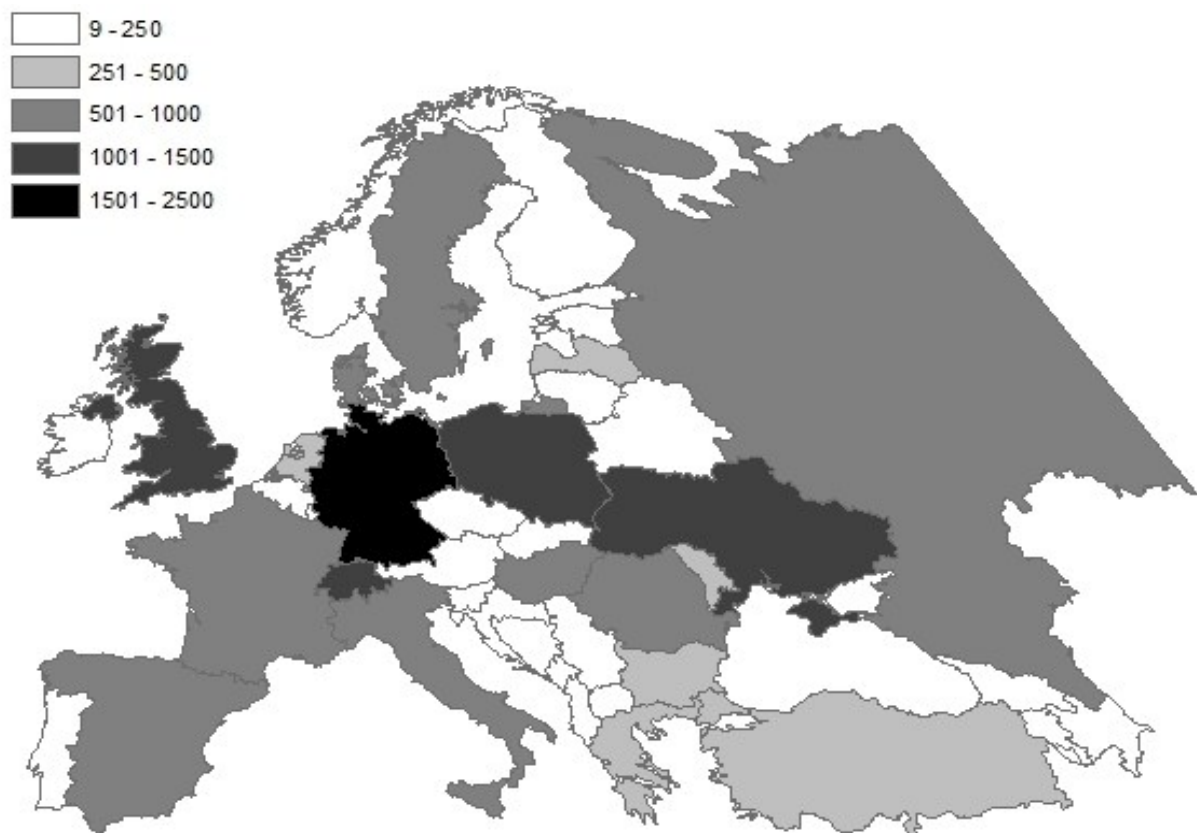


Figure 2.2 Map showing the spatial distribution of zooarchaeological records across each country of Europe.

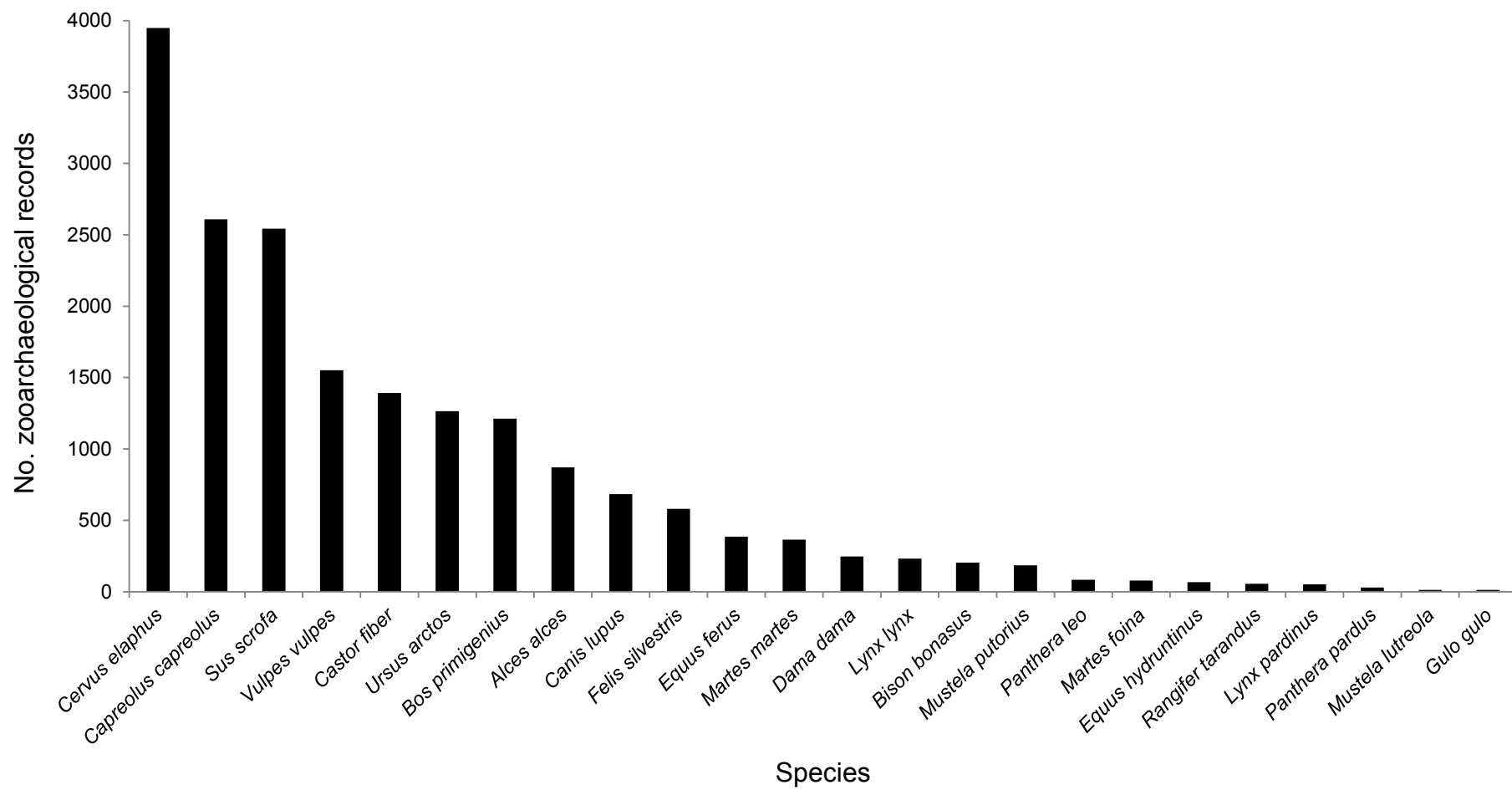


Figure 2.3 Number of zooarchaeological records for each species across the Holocene.

3. Bias in the Holocene zooarchaeological record

3.1 Abstract

Bias is an accepted component of all species occurrence data, in particular past bone assemblages. On a site-by-site basis, researchers have been predominantly concerned with taphonomic bias and how this can be minimised. However, when data are pooled into larger scale analyses, patterns of intrinsic and extrinsic bias in faunal assemblages are rarely considered, particularly in continent-wide analyses that may include data from numerous disparate studies. This chapter investigated intrinsic (ecological) and extrinsic (spatial and temporal) sources of bias in a Holocene dataset of zooarchaeological records of large mammals across Europe. Diet breadth and a simplified measure of trophic level were found to significantly influence the abundance of each species recovered from the zooarchaeological record, although body mass was also closely correlated with zooarchaeological abundance. No source of spatial bias was identified across the dataset. The precision of dating was found to vary over time, and possible implications of this for interpreting patterns of faunal change over time are discussed. This study represents the first of its kind to identify and quantify bias across a large continent-wide zooarchaeological dataset. The results have relevance to a wide range of datasets obtained from fossil and non-fossil records used in macroecology, zooarchaeology and palaeontology.

3.2 Introduction

Historical and prehistoric data are crucial for understanding past patterns of biodiversity. For the Holocene Epoch, the zooarchaeological record is the major source of information on mammalian ecology and diversity. Unlike the fossil record, which comprises naturally accumulated assemblages, the zooarchaeological record relies on past human accumulation to generate faunal assemblages. However, as with all faunal deposits, it is both uneven and incomplete (Behrensmeyer *et al.* 2000), and therefore is unlikely to fully or accurately represent the actual source communities present during the period of time being studied. A number of processes take place during the deposition and excavation of faunal assemblages that affect the taxonomic composition, abundance and location of the faunal material that is eventually recovered from sampling. It is vital to understand, and where possible quantify, such biases in order to be able to correctly interpret analyses based on this type of species occurrence data.

3.2.1 Sources of bias

Phenomena that affect what is eventually recovered and interpreted from the zooarchaeological record are generally classified as either first order (pre-excavation) or second order (post-excavation) changes (Reitz and Wing 2004).

3.2.1.1 First order changes

First-order changes refer to those that occur from the moment the remains are discarded or buried until the moment of excavation. It is generally the task of the discipline of taphonomy, literally meaning the science of the laws of burial (Lyman 1994), to evaluate such modifications. These include biotic disturbances from other organisms, for example trampling, scavenging and burrowing animals or plant root growth, as well as abiotic disturbances such as wind, rain, floods and heat. Conditions that promote preservation in the zooarchaeological record are those which limit disturbance, restrict bacterial growth and remain stable, which tend to be environmental extremes such as complete submergence in water, the desiccation of a cave, or the cold of permafrost.

Intrinsic qualities of the faunal deposition can also affect its survival, for example in general the largest, hardest, densest bones and teeth survive best in response to weathering, burial and decomposition (Behrensmeyer *et al.* 1979; Lyman 1994) meaning that the relative representation of different-sized species and taxonomic groups in the zooarchaeological record may be biased. Other ecological traits are less well understood in terms of their role in controlling relative patterns of preservation in bone deposits but studies have suggested that e.g. trophic guild (Carbone *et al.* 2009) and habitat (Johnson 2002) can affect the frequency with which different species occur in bone deposits.

However, Damuth (1982) observed the paradox that it is often not possible to demonstrate or quantify the introduction of bias on abundance and species richness in the fossil record due to a lack of a priori knowledge of those source communities to begin with. This is compounded by the fact that current species assemblages themselves are not easy to generalise. For example, the predictive power of body size-abundance relationships, which are sometimes used to predict past assemblage abundance (e.g. Damuth 1982; Turvey and Blackburn 2011), varies markedly across taxonomic groups (Peters and Wassenberg 1983; Brown and Maurer 1987; Nee *et al.* 1991; Cotgreave 1993; Russo *et al.* 2003, White *et al.* 2007).

One further fundamental question that is rarely addressed with regards to Late Quaternary, particularly Holocene, ecosystems is whether extant communities are in fact 'natural' communities or whether they are human-biased as well. More specifically, can we assume that postglacial fossil communities were similar to present-day communities of mammals in the ecological properties of their structure and composition (Damuth 1982) and thus would such a direct comparison between the two be advisable? For example, the large mammal fauna of northern Eurasia and North America has been preferentially hunted throughout the Late Quaternary (Martin and Klein 1984; Turvey 2009b) and the selective removal of certain species and populations of species has arguably left these modern-day mammal communities in a state of non-equilibrium. Indeed there is potentially a wider debate to be had over what a 'baseline' community for comparison would constitute since ecological systems appear to have constantly shifted in response to changing environmental and anthropogenic

conditions (Alagona *et al.* 2012). If comparison between extant and fossil assemblages is undertaken, such analyses must clearly be chosen carefully, not only for comparability but also in order to address the above issues of faunal representation, sample size and spatial scale.

The zooarchaeological record should also be distinguished from natural fossil (palaeontological) assemblages. In general the latter assemblages have been deposited by 'natural' (non-anthropogenic) means, for example from animals dying, decomposing and being buried and preserved by natural sedimentological processes, being trapped in tar pits such as those at La Brea, or through accumulation of prey species by non-human predators such as raptors. By contrast, zooarchaeological assemblages are by definition found in human (archaeological) contexts that reflect prehistoric or historical processes of animal exploitation from hunting to herding to domestication. These deposits can constitute killing sites, refuse pits, or deliberate burial. A human selection filter has therefore contributed towards the composition of these faunal assemblages in addition to reflecting which species were formerly present in the environment, and it may not be easy to disentangle these two factors.

Such a 'human filter' could take a number of forms. Human demographic change throughout the Holocene (McEvedy and Jones 1978; Shennan and Ediborough 2007; Goldewijk *et al.* 2010) and changes in hunting technology are likely to have affected the extent to which different species were exploited. The domestication of species altered patterns of exploitation of wild animals through the taming and removal of individuals from wild populations for breeding and through the gradual introduction of a controllable meat source, although shifts in subsistence strategies were not necessarily a straightforward linear process (Buitenhuis 1990; Davis 2005). Social differences can also be expressed through food, and research has shown that different game taxa for example fell in and out of popularity with social change and according to socioeconomic class (Reitz 1987; Ashby 2002). These and other anthropogenic factors could all affect the final composition of zooarchaeological assemblages.

3.2.1.2 Second order changes

Second-order changes describe those that affect the assemblage from the point of excavation, for example sampling strategy and excavation location. Any biases arising from these processes are partly controlled for by standardised excavation methods (e.g. Barker 1993), but the sampling strategy that yields occurrence data from the zooarchaeological record is always partly opportunistic.

Archaeological sites can be discovered in a variety of ways. They can be actively searched for in known areas of cultural interest, or in areas where archaeological and fossil material are known to survive well; they can be found accidentally; and they can be found from salvage archaeology (Drewett 2012). This means that numbers of fossils discovered and processed are likely to vary across space. The various countries of Europe also differ greatly both physically (topography, underlying geology, urban versus rural areas etc.) and in their political and economic histories, all of which could affect the amount of excavation, i.e. sampling, undertaken. Therefore there may be

explicit spatial bias in the spread of zooarchaeological sites across Europe that may not reflect underlying natural distributions.

Excavation methods within a site should aim to uncover all remains within an area but there are many historical accounts of the preferential collection of larger 'charismatic' species of interest (Turvey and Cooper 2009). Even if this is not the case, adequate sampling strategies such as sieving must be used to recover remains of smaller vertebrates and invertebrates. Once recovered, smaller bones and teeth are likely to be more difficult to identify to species level (Klein and Cruz-Urbe 1984) so that the quality of final data may be biased towards larger species. However the implications of using finer scale techniques, such as sieving, on our understanding of past species richness is increasingly being acknowledged and such methods are now widely used (Gordon 1993; James 1997; Zohar and Belmaker 2005).

3.2.2 Temporal change

The concept of time in archaeology is necessarily tied to the scale and nature of the research being undertaken, in other words it is neither linear nor absolute (Ramenofsky 1998). In order to be able to measure temporal dimensions, archaeologists necessarily construct chronologies by dividing time into measurable units. By definition, such divisions will be conceptual and to some degree imposed and may vary through time; however, this 'arbitrariness' does not mean that the process is illogical or random (Ramenofsky 1998). 'Absolute' and 'relative' refer to the accuracy of dating methods in archaeology. With absolute dating (e.g. radiocarbon) only one event is needed and statistically derived age estimates are associated with an object. With relative dating, a minimum of two events are required and they are ranked relative to each other. In practice, and with a wealth of archaeological information, a combination of the two dating methods is usually used, with absolute dating often used to support relatively constructed chronologies for well-known archaeological periods and cultures. Whilst, statistically speaking, absolute methods generally derive more accurate dates, they are not necessarily more precise, concepts which should not be conflated. Precision here refers to the length of the time estimate given, with a shorter interval being more precise.

The variety of dating methods used for different records in the zooarchaeological database means that the precision of dating may vary across time. Radiocarbon dating has been widely used to track the effect of climate and humans on faunal composition and extinction during important periods of environmental change such as the Pleistocene-Holocene boundary (e.g. MacPhee *et al.* 2002; Stuart *et al.* 2004; Guthrie 2006). However for the Holocene Epoch itself, where an ameliorated climate facilitated major changes in human activity, research has tended to focus on how faunal assemblages reflected human society and culture (e.g. Russell 2012) rather than on dynamics of faunal communities themselves. As a consequence there is often little incentive to date individual bones and zooarchaeological remains are often simply associated with the age of the archaeological site, which could have been dated by absolute or relative means. Thus a bone could be dated anything from 'Late Mesolithic', a period potentially spanning a couple of thousand years, to a specific cultural

period, definable to a couple of hundred years. The extent of the disparity in dating methods and any bias this may place on the dating of bones over time should therefore also be carefully considered.

In short, it cannot be assumed that zooarchaeological assemblages faithfully reflect natural faunal source communities, and they should be critically assessed for such bias prior to further analysis. Taphonomic bias on an individual site or sampler basis could also be further distorted when considered across a number of individual sites. With this concern in mind, this chapter will investigate possible patterns of intrinsic (ecological) and extrinsic (spatial and temporal) sources of bias across the current Holocene dataset of mammal faunal occurrences.

3.3 Methods

The Holocene database of mammalian zooarchaeological records, as described in Chapter 2, was used as the basis for all analyses, and the following sources of bias were examined for their possible effects on the abundance of different species in the zooarchaeological record over space and time (Chapter 2, figs. 2.2, 2.3). All statistical analyses were performed in R Studio, version 0.94.105 (RStudio 2012) using the package “MASS”. All spatial data were calculated in ESRI ArcMap version 9.3 (ESRI 2008) using the Arc Toolbox.

3.3.1 Intrinsic bias

The number of zooarchaeological records for each species was converted into the proportion of sites occupied across its extent of occurrence (a minimum convex polygon enclosing all sites). This was to account for i) species' differing range sizes which might skew the overall abundance of each species, and ii) areas of Europe which had low densities of zooarchaeological sites and which might artificially lower abundance for the species' ranges that fell within these areas. As a proxy measure for zooarchaeological abundance, 'proportion of occupied sites' will hereafter be referred to as 'abundance'.

The wild horse (*Equus ferus*) was excluded from this analysis because accurate records for this species only covered the first half of the Holocene (due to identification problems with its domestic counterpart in the later Holocene) and therefore were not comparable to other species. Fallow deer (*Dama dama*) was also excluded because, as a largely introduced species, its range was artificially fragmented across Europe and this made it impossible to calculate a native range extent using extent of occurrence. Furthermore, because the abundance and distribution of this species are known to have been determined by active introduction beyond its natural range, this constituted an additional known human bias that all other species were not necessarily subject to.

Zooarchaeological abundance of all species was compared with nine ecological variables that were predicted to potentially influence whether a species might be subject to human exploitation and

appear in the zooarchaeological record. These were body mass (kg), diet breadth (a categorical variable from 1-8, with 1 representing a restricted diet consuming only one category of food and 8 representing a highly varied diet consuming up to eight different categories of food), trophic level (a categorical variable from 1-3), activity cycle (whether a species was nocturnal or diurnal), and reproductive rate variables. Specific reproductive rate variables were chosen according to the criteria and results outlined in Bielby *et al.* (2007), which highlighted that life history co-varied along two largely independent axes based on i) timing and ii) output. The variable from each cluster that explained the highest proportion of the variation across both Carnivora and Artiodactyla was chosen: these were, respectively, interbirth interval (days) and litter size. Life history data were taken from the PanTHERIA database (Jones *et al.* 2009). Data for the extinct aurochs (*Bos primigenius*) were taken from Smith *et al.* (2003) and Van Vuure (2005) and where specific variables were lacking European bison (*Bison bonasus*) data were utilised as a comparable species (Van Vuure 2005) from Jones *et al.* (2009). Body mass was logarithmically transformed for analysis. Additional traits investigated were a simpler measure of trophic guild (a categorical herbivore/carnivore variable), current IUCN Red List status (a ranked categorical variable from 0-6, where 0=Least Concern and 6=Extinct), and whether a species had a domestic counterpart (a categorical yes/no variable).

The determinants of abundance were analysed for all independent variables using univariate general linear models (GLMs) with quasibinomial errors to account for the dependent variable being a proportion and displaying overdispersion (extra unexplained variation). All significant terms were then modelled in a multivariate quasibinomial GLM and interactions between the variables tested. Nonsignificant terms were deleted in order to produce a minimum adequate model that explained abundance only in terms of statistically significant independent variables and any interactions.

In order to assess whether any relationship between abundance in the fossil record and body mass could be attributed to taphonomic bias, evidence for the current biological relationship between abundance and body mass in mammals was investigated. Ecological data on population density and body mass for global populations of mammals were taken from Damuth (1987). Species were chosen whose average body mass ranged between 0.5kg and 700kg, and within the orders Artiodactyla, Carnivora and Perissodactyla (representing the main body size distribution and orders present in the Holocene dataset). This order of magnitude was also deemed sufficient to overcome any biasing effects on the body size-abundance relationship of using small orders of magnitude (Blackburn and Gaston 1997). The data were separated out geographically and data from North America was chosen for direct comparison with the European zooarchaeological record as the most intact and analogous present-day ecosystem to the Holocene of northern Eurasia. In order to investigate the effect of sample size on the relationship, data from all continents were also pooled and compared. Analyses were carried out using linear regressions.

In order to investigate possible effects of trophic guild, all three datasets (Holocene Europe, Damuth North American and Damuth all continents) were then separated into herbivores and carnivores, and

general linear models and linear models for abundance and body mass were repeated across all six separate datasets. Confidence intervals were calculated for all slopes as another method for comparison between the different models. If confidence intervals overlapped, it would be assumed that the slopes in question (and therefore the distributions) did not significantly differ.

3.3.2 Extrinsic bias

3.3.2.1 Spatial bias

Inspection of a map of the spatial spread of data (see Chapter 2, figs. 2.1, 2.2) suggested that numbers of zooarchaeological records differed between countries and that central and western Europe appeared to have higher representation. It was suspected that this might be related to country wealth and the resources available for zooarchaeological research. In order to investigate this, total number of zooarchaeological records (considered to represent a proxy of research output) was calculated for each country. In case the number of zooarchaeological records reflected incidental high output from a few sites rather than overall research effort, a Pearson's correlation coefficient was carried out to test the relationship between numbers of zooarchaeological records and zooarchaeological sites per country. This was found to be extremely highly positively correlated (Pearson's $r = 0.914847$, $df = 38$, $p < 0.05$), and so number of zooarchaeological records remained as the chosen metric. Whilst there are many economic measures of wealth, GDP measures the market value of all goods and services of a country, i.e. a country's total economic activity, and is therefore considered an appropriate proxy measurement of a country's wealth. However, it has been demonstrated that a country's land area, GDP and population are all positively correlated (Panahi 2010), meaning that raw data on numbers of zooarchaeological records and GDP might not be suitable as both might show collinearity with land area. Regression analysis confirmed that country land area and GDP across Europe did correlate (Pearson's $r = 0.3493265$, $df = 38$, $p < 0.05$). Therefore, i) total number of zooarchaeological records was corrected for land area and converted into a measure of density of records for each country; and ii) GDP per capita was used rather than GDP. Data on GDP per capita for all countries were taken from the World Bank website (2013). The most recent data available (2010) were used. The relationship between the density of zooarchaeological records and the GDP per capita for each country was analysed using a GLM with quasipoisson errors to account for overdispersion. GDP per capita was logarithmically transformed for analysis.

In order to investigate whether the spatially uneven spread of data could be related to Europe's variable topography, a high-resolution 30-arc seconds (c.1km) elevation map was downloaded from the WorldClim database (2012). This was clipped to a map of the European countries being investigated and zonal statistics were used to calculate the summed elevation values of each grid cell for each country. This was measured as metres above or below sea level, as a positive or negative integer respectively. This value was then divided by the country area (km^2) to give the average elevation for each country. The relationship between the number of zooarchaeological records and

the average elevation for each country was analysed using a negative binomial GLM to account for considerable overdispersion. Average elevation was logarithmically transformed for analysis.

A random elevation profile for the zooarchaeological dataset was also compared to that of the underlying GIS elevation layer for Europe in order to see whether there were differences in the overall range of values between the two and to check that the average elevation was not being biased by widely outlying values. The elevation of the 30-arc raster square at each zooarchaeological data point was calculated and then randomly sampled 10000 times to produce an elevation profile for the dataset which was then plotted as a histogram. This was repeated for the WorldClim elevation layer for Europe, with each 30-arc raster square again denoting the individual sampling units.

3.3.2.2 Temporal bias

In order to examine any changes or patterns in dating precision over time the lower interval and upper interval date was plotted (by midpoint) for each zooarchaeological record. These data were plotted against a straight line from the oldest to the most recent midpoint to represent a linear increase in the number of zooarchaeological records over time; the data were then compared to this line in order to see how the accumulation of records varied through the Holocene. It should be noted that a radiocarbon date does not represent a midpoint with error, rather it is a complex measure of statistical probability; however these records were by far the least numerous and it was the interval rather than the midpoint that was the most important aspect of the data for analysis.

3.4 Results

3.4.1 Intrinsic bias

Univariate analysis indicated that zooarchaeological abundance was closely but not significantly correlated with body mass (regression estimate $\pm$ standard error = 3.2788 ± 1.2128 , $p = 0.0706$) although when plotted there was a positive relationship in the data (fig. 3.1). Interbirth interval, litter size, activity cycle, IUCN status and whether each species had a domestic counterpart were all non-significant. Diet breadth, trophic level and trophic guild (see Appendix 6) were all significantly positively correlated with abundance.

However when these variables were put into the full multivariate GLM, there were no significant interactions and trophic level was lost as a significant variable. For the simplified trophic guild herbivore/carnivore variable, the level of herbivore remained significantly positively related to abundance. For diet breadth, levels 1, 2, 3, 5, and 6 were represented in the data but in the multivariate model only levels 5 and 6 were found to be significantly positively related to zooarchaeological abundance (Table 3.1).

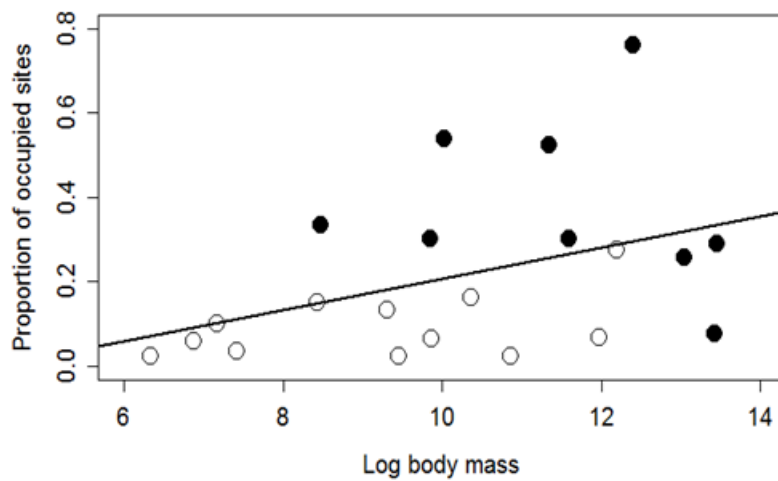


Figure 3.1 The relationship between proportion of occupied sites in the zooarchaeological record in which a species occurs and log body mass. Data for body mass were log transformed. The regression line is derived from the univariate GLM model with quasibinomial errors; closed circles represent herbivores and open circles represent carnivores.

Table 3.1 Minimum adequate GLM of proportion of occupied sites in which a species is found.

	<i>a</i>	SE	<i>t</i>	
Intercept	-2.51252	0.64787	-3.878	**
Trophic guild (Herbivore)	1.5801	-0.53935	2.93	*
Diet Breadth (5 food categories)	2.09869	0.62436	3.361	**
Diet Breadth (6 food categories)	2.6177	1.04805	2.498	*

* $p < 0.05$, ** $p < 0.01$

For the dataset of global mammal population density estimates (Damuth 1987), the North American subset of data was closely but not quite significantly negatively associated with body mass (-0.3160 ± 0.1566 , $p = 0.0544$). When data from all continents was pooled, population density became highly significantly negatively correlated with body mass (-0.27031 ± 0.08892 , $p < 0.01$) (fig. 3.2). Ninety five percent confidence intervals for the Holocene dataset and the North American dataset overlapped, meaning that the slopes were not significantly different. However, they did not overlap for the Holocene dataset and the dataset for all continents (Table 3.2), indicating that these two slopes were significantly different.

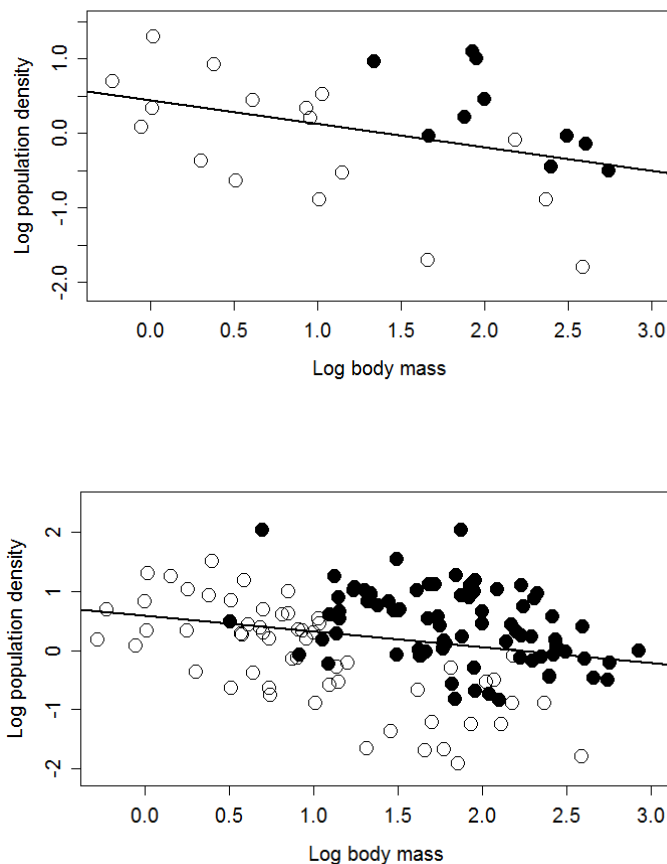


Figure 3.2 The relationship between population density and body mass in the orders Artiodactyla, Carnivora and Perissodactyla, within the body size range 0.5-700 kg. Data are for North America (top plot) and all continents pooled together (bottom plot) from the ecological dataset published by Damuth (1987). Population density and body mass were log transformed for clarity. Regression lines were taken from the linear models. Closed circles represent herbivores and open circles represent carnivores.

When the data were split into trophic guilds (herbivore/carnivore) both Damuth carnivore datasets showed a statistically significant negative body mass-abundance relationship (Table 3.2). The carnivore subset of the Holocene data showed no statistically significant result but the slope was positive and 95% confidence intervals did not overlap with either slope from the Damuth carnivore datasets indicating that it was significantly different. Both herbivore subsets of Damuth data also demonstrated a statistically significant negative body mass-abundance relationship (Table 3.2). The herbivore subset of Holocene data showed no statistically significant result but the slope was also negative and overlapped with both slopes from the Damuth herbivore datasets indicating that it was not significantly different.

Table 3.2 Slopes and 95% confidence intervals of the linear models of proxies of abundance and body mass for the Holocene zooarchaeological dataset and the ecological dataset published by Damuth (1987).

	<i>a</i>	SE	df	CI 2.5%	CI 97.5%	
All data						
Holocene zooarchaeological record	0.21	0.11	20	0.00082	0.43989	
Damuth North America	-0.32	0.16	25	-0.00076	0.07462	.
Damuth all continents	-0.27	0.09	134	-0.44617	-0.09444	**
Carnivore subset						
Holocene zooarchaeological record	0.15	0.13	12	-0.10970	0.41039	
Damuth North America	-0.70	0.19	15	-1.09655	-0.29830	**
Damuth all continents	-0.88	0.12	55	-1.11843	-0.64989	***
Herbivore subset						
Holocene zooarchaeological record	-0.17	0.23	7	-0.64294	0.28798	
Damuth North America	-0.94	0.33	8	-1.71314	-0.17379	*
Damuth all continents	-0.47	0.13	77	-0.72917	-0.22065	***

. $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

3.4.2 Spatial bias

There was no statistically significant association between the density of zooarchaeological records and GDP per capita of a country (0.3731 ± 0.3106 , $p > 0.05$). There was also no relationship between the number of zooarchaeological records and the average elevation of a country (-0.2004 ± 0.1596 , $p > 0.05$). Furthermore, histograms of randomly sampled elevation profiles for the Holocene dataset and the underlying GIS elevation layer for Europe showed almost no difference (fig. 3.3).

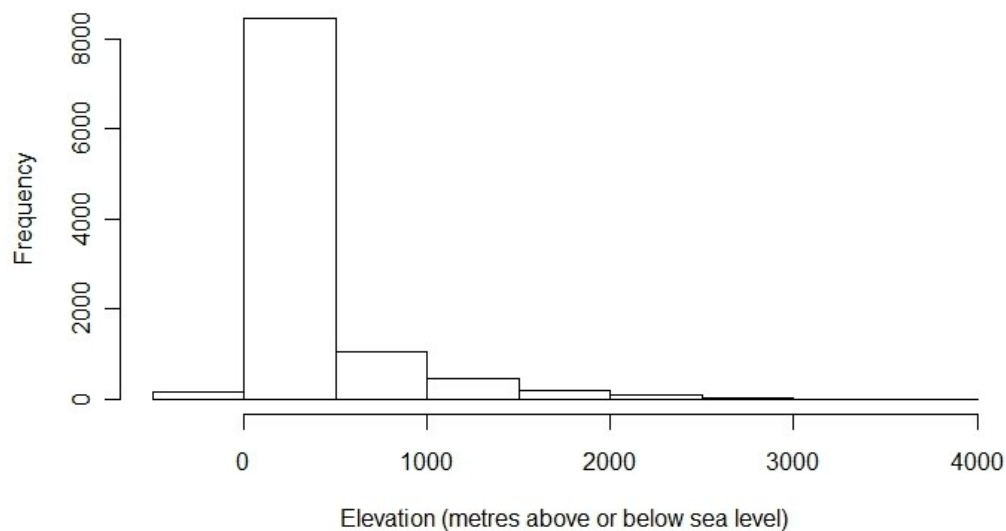
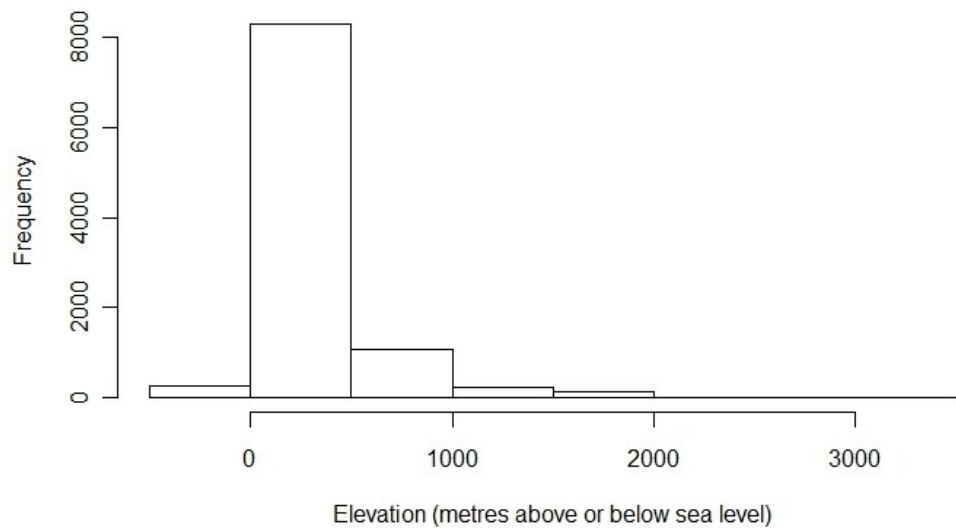


Figure 3.3 Histogram of 10,000 random samples of the elevation of Holocene zooarchaeological records in Europe (top) and histogram of 10,000 random samples of raster grids from an ArcMap layer of European elevation (bottom).

3.4.3 Temporal bias

The precision of dating for records from different parts of the Holocene was uneven. In general, the average time interval for each zooarchaeological record narrowed closer to the present, with this shift becoming particularly marked around 0 BC/AD (fig. 3.4). Overall the accumulation of records was initially slow during the early Holocene, was relatively steady for much of the mid-Holocene and increased somewhat in the later Holocene nearer the present.

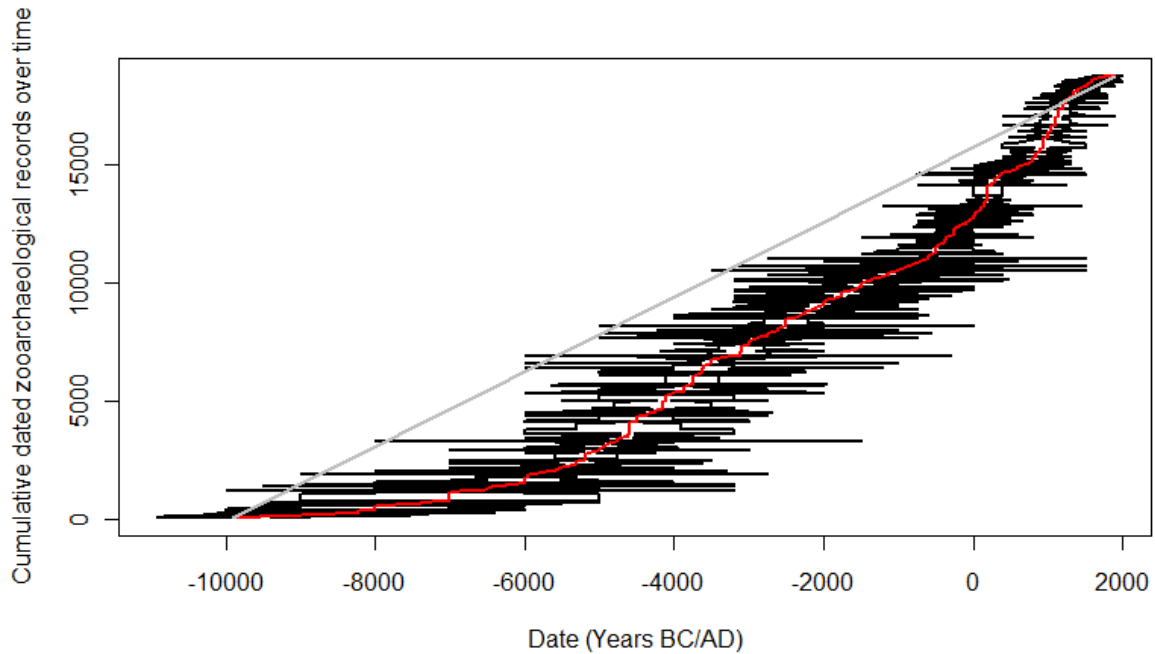


Figure 3.4 Graph showing i) the ranges of estimated dates for all zooarchaeological records through time and ii) the accumulation of records in the zooarchaeological record through time. The grey slope denotes a theoretical linear rate of accumulation.

3.5 Discussion

In order to track species distributions through time various sources of species occurrence data must be employed, from present day monitoring to museum and historical records through to the zooarchaeological and palaeontological record. However all are likely to display some degree of bias in their compilation. Whilst bias has been studied in ecological (e.g. Graham *et al.* 2007; Phillips *et al.* 2009), historical (e.g. Hortal *et al.* 2008; Boakes *et al.* 2010) and palaeontological (e.g. Koch 1978; Benton *et al.* 2000; Benton *et al.* 2011) datasets, this study represents the first attempt to directly quantify multiple sources of bias in a large zooarchaeological dataset.

3.5.1 Intrinsic bias

Zooarchaeological abundance was significantly correlated with the level of 'herbivore' in the trophic guild variable. The most abundant and larger species were also generally herbivores and the least abundant and smaller species were carnivores (fig. 3.1). The higher abundance of herbivores could reflect the fact that humans were preferentially hunting these species, it could reflect underlying ecological reality, or it could reflect a mixture of both. The likelihood that larger-bodied vertebrates have been a primary focus of prehistoric human hunting effort is supported by the pattern of terrestrial and insular extinctions following human arrival or technological change across the globe during the Late Quaternary, as well as by studies of prey selection by modern-day subsistence hunters (Lyons *et al.* 2004; Turvey 2009b). Whilst the increased extinction vulnerability of large-bodied mammals is

probably as much related to associated slow reproductive life histories as body size *per se*, such species also tended to be diurnal and terrestrial and so would have more frequently come into contact with humans (Johnson 2002). However, the results from all Damuth datasets (Table 3.2) demonstrated that body mass scaled inversely to population density in natural populations, a relationship that has also been demonstrated elsewhere (Damuth 1981; Cotgreave 1993). Thus we would have expected fewer large species if zooarchaeological abundance reflected underlying reality, suggesting that the zooarchaeological dataset did appear to reflect an overall bias towards an abundance of larger species.

However, although a positive relationship, zooarchaeological abundance and body mass were not quite significantly associated meaning that this conclusion can only be tentatively suggested. When using North America-only data to provide a close ecological approximation for the Holocene record this was also nearly significant but the power of the relationship was likely reduced by the smaller sample size and smaller range of body masses. The two slopes, despite being negative and positive respectively, were not significantly different from one another (Table 3.2), probably because neither was significantly different from zero. Thus paucity of data points may be leading to a Type 2 error, preventing the ability to detect this relationship more clearly, a problem that has been noted in previous large-scale analyses of fossil mammal assemblages (e.g. Jernvall and Fortelius 2002). This is further supported by the fact that the slope for the zooarchaeological record did differ significantly from the slope for the full Damuth dataset which contained a greater order of magnitude of body masses. Therefore whilst the zooarchaeological data did appear to indicate a degree of size bias, this relationship would be better tested across a dataset including more species, in particular herbivores, and a wider range of body size classes, which has previously been demonstrated to strengthen body mass-abundance relationships (Blackburn and Gaston 1997).

This picture was further complicated at the trophic guild level, where the carnivore subset of zooarchaeological data demonstrated a statistically different pattern from the Damuth datasets, whilst the herbivore subset showed no difference to the Damuth datasets. This suggests that whilst body mass appeared to be the primary determinant of carnivore abundance in the zooarchaeological record, this may not have been the only, or even dominant, factor influencing herbivore abundance. Abundance in the zooarchaeological record was also significantly correlated with levels 5 and 6 in the diet breadth variable, i.e. species with a more varied diet. Generalist, abundant species are thought to have a lower extinction risk than rare, specialist species both in the palaeontological record and the present day, although this trait may co-vary with other extinction-reducing traits (McKinney 1997; McKinney and Lockwood 1999). Thus it makes sense that such species might consistently appear in higher abundance in the zooarchaeological record since they could be at lower risk of disappearing from source assemblages in local landscapes and potentially be more resilient to hunting pressure. Indeed, among the most abundant herbivores were red deer (*Cervus elaphus*), and wild boar (*Sus scrofa*) which scored highest for diet breadth and were also among the smallest herbivores. Red deer in particular was dominant in the zooarchaeological record throughout most of the Holocene in

Europe (Sommer *et al.* 2008) and was even eventually afforded protection for hunting in Medieval law in Britain (Ashby 2002).

Perhaps also for this reason species abundance in the zooarchaeological record did not correlate with IUCN extinction risk status, the opposite of which might have been expected if species were historically heavily hunted. However, this was also probably linked to the fact that IUCN categories represent a species' present day global status so does not take into account the historical continent-wide extirpation of species such as European bison, lion (*Panthera leo*) and leopard (*Panthera pardus*); furthermore European bison has been reintroduced and is now listed as 'Vulnerable', rather than its past status as Extinct in the Wild which was reflected in its disappearance from the zooarchaeological record during the Modern period.

3.5.2 Spatial bias

The original database of zooarchaeological records lacked data from regions such as the western Balkans with turbulent political histories that had hampered past research effort (Robert Sommer, Christian-Albrechts-Universität zu Kiel, personal communication, 2010). During subsequent data collection fewer zooarchaeological records were obtained from these countries, exacerbated by less accessible literature, in comparison with other areas of Europe. Therefore it was predicted that poorer countries produced less zooarchaeological research, leading to a degree of spatial bias across the dataset. However, contrary to expectations, the relative wealth of a country did not significantly influence research output across European countries once the size of the country was taken into account. This is encouraging in terms of not having arbitrary data gaps for less wealthy countries. This pattern may be partly due to the fact that archaeology is a fairly international endeavour and therefore foreign academics will often fund and carry out, or collaborate on, excavations in countries other than their own, for example there is a strong international academic presence in Anatolian archaeology (e.g. Zeder 2006a) and parts of the Caucasus (e.g. Chataigner 1995). Furthermore, even where research funds are reduced, countries can nonetheless have strong traditions of academic research and achieve relatively high research output with few people, for example as was found in Armenia where only one previous and one current zooarchaeologist worked (Mejlumian 1988; Ninna Manaserian, Institute of Zoology, Armenian National Academy of Sciences, personal communication, April 2011). A final reason may be that the literature research covered relatively obscure, or at least difficult-to-obtain, grey literature in numerous European languages as well as research published in high profile international journals and therefore reached a range of research repositories, not limited to those dependent on or linked to higher levels of funding.

The spatial spread of the Holocene dataset was also not biased by elevation. Countries at a high average elevation, such as Switzerland and Austria, nonetheless contained comparable numbers of zooarchaeological records to countries at a lower elevation. Elevation profiles showed that zooarchaeological records were present up to 2000 metres above sea level (m.a.s.l.) but were generally absent above this (fig. 3.3). Whilst the overall elevation profile for Europe did reach 3000

m.a.s.l., over 95% of Europe was represented up to 2000 m.a.s.l. (fig. 3.3) and thus even if elevation were to have had a biasing effect, this may not have been evident and would have a minimal effect on interpretation of zooarchaeological data.

3.5.3 Temporal bias

The precision of dating for zooarchaeological records varied across the Holocene, reflecting the mix of absolute and relative methods used to measure time in archaeology across a large dataset (see Chapter 2). In an ideal scenario all zooarchaeological records would be radiocarbon dated in order to ensure that chronologies for subsequent investigations into timings of faunal turnover and extinction were as accurate as possible. However given the sheer quantity of data generated from archaeological sites and the costs involved in absolute dating, this is rarely an option. The nearer to the present-day that archaeological research is conducted, the more confident archaeologists can generally be at assigning a date to finds. Cultural and archaeological chronologies are often constructed tightly enough within the past couple of thousand years to give a satisfactorily precise estimate without resorting to absolute methods. This probably helps to explain why records were assigned increasingly specific dates nearer to the present (fig. 3.4). Non-specific archaeological designations (Mesolithic, Neolithic etc) are generally the broadest catch-all archaeological descriptions and therefore tend to be the most imprecise. Archaeological periods denote changes in technology and subsistence, and due to the general exponential increase in technological change through time, each subsequent archaeological designation is generally shorter than the preceding one, meaning a decrease in precision the farther back in time using broad relative methods. This too may help explain why time interval lengths decreased towards the present.

Intermittent periods of increasing accumulation of zooarchaeological records (fig. 3.4) could reflect prehistoric human population increase, with humans leaving a larger archaeological footprint and traces of evidence on the landscape to be found and excavated. Exacerbated pressure on wildlife populations by an expanding human population could subsequently have increased numbers of zooarchaeological records found within these sites and which seemed not to abate, even after domestication around 5000 BC. On the other hand it has been demonstrated that regardless of prior distributions, a constant taphonomic influence on the archaeological record will produce a positive curvilinear frequency distribution through time (Surovell and Brantingham 2007); in other words, younger components will always be more abundant than older components. This is due to the greater likelihood of destruction for faunal or archaeological remains the longer that they are exposed to taphonomic processes and to the greater detectability of stratigraphically higher samples, but is often erroneously used as evidence of past exponential population growth.

On the whole, bias in the zooarchaeological database varied depending on its source, exacerbated by often substantial difficulties in its quantification. Intrinsic bias related to the relative abundance of different species in the zooarchaeological record was difficult to detect due to a small sample size of species and the dual effects of taphonomy and human selection bias. However the data did suggest

some size bias in favour of larger and generalist species more frequently appearing, and/or surviving, in the zooarchaeological record. Whilst the geographical spread of records was uneven, the underlying source of this bias could not be detected, but it was not due to socio-economic reasons or underlying topography. Zooarchaeological records were also not spread evenly through time, but again there was no strong biasing pattern that appeared to be influencing the temporal distribution of data. However it should be acknowledged that due to the large quantity of relatively dated bones the precision of dating improved nearer to the present and therefore chronologies can probably be more precisely constructed for the late Holocene than the early Holocene. Furthermore probable taphonomic effects meant that overall quantities of bones were higher for the latter part of the Holocene but which may not reflect underlying source communities.

3.6 Conclusion

Bias occurs when some parts of a population are more or less likely to be sampled than others. This study examined several sources of bias in a large zooarchaeological database. However, it goes beyond a narrow focus on taphonomy to look at additional sources of spatial and temporal bias introduced by the accumulation of a large number of individual records into a single database as well as the added human filter bias inherent in the archaeological record. Accepting inevitable sources of bias in large zooarchaeological or other species occurrence datasets does not reduce their usefulness, rather such an exercise is crucial for ensuring that interpretations of analyses based on such data are made in full knowledge of the factors that might shape outcomes and results.

Chapter 4. Pleistocene relicts: extinction dynamics of a late surviving equid *Equus hydruntinus* in the Holocene of Europe

4.1 Abstract

Equus hydruntinus Regalia, 1907 is an extinct Eurasian equid. It was widespread in the Late Pleistocene in Europe and southwest Asia but its distribution became restricted to southern Europe in the Holocene and it is thought to have become extinct in the Late Holocene. Following confusion over its taxonomic status, it is now confirmed to be related to hemionines based on morphometrics and genetics, and is most closely related to the extant Asiatic wild ass (*E. hemionus*). The limited number of publications on *E. hydruntinus* has focused predominantly on its taxonomy and distribution in the Late Pleistocene. However, there is still very little understood about its Holocene distribution and extinction, despite it representing one of Europe's few globally extinct Holocene megafaunal mammal species. This chapter therefore summarises Holocene zooarchaeological occurrence data for the species and analyses patterns of its distribution and extinction. These data challenge historical accounts of a late survival of *E. hydruntinus* into the medieval period in Spain and suggest that post-glacial climate-driven vegetational changes were a primary factor responsible for its extinction, leading to the isolation of small remnant subpopulations that may have been increasingly vulnerable to human exploitation. This study contributes to a more nuanced understanding of Late Quaternary species extinctions in Eurasia, suggesting that they were temporally staggered and distinct in their respective extinction trajectories.

4.2 Introduction

Rapid climatic change at the end of the last ice age glaciation was reflected by faunal turnover from predominantly cold-adapted to warm-adapted species in Europe. Faunal change at the Pleistocene-Holocene transition is now well documented (Benecke 1999a; Coard and Chamberlain 1999). However this process did not occur entirely uniformly across Europe due to climatic variation and the existence of refugia across the continent which influenced the ability of species to survive in different regions (Hewitt 1999; Stewart and Lister 2001; Stewart *et al.* 2010). As a consequence not all species adapted to dry, open Late Pleistocene environments became extinct immediately following the Last Glacial Maximum (LGM), and several species such as mammoth (*Mammuthus primigenius*), giant deer (*Megaloceros giganteus*), muskox (*Ovibos moschatus*), reindeer (*Rangifer tarandus*) and wild horse (*Equus ferus*) persisted into the Holocene of northern Eurasia (Stuart 1999; MacPhee *et al.* 2002; Stuart *et al.* 2004). The European wild ass (*E. hydruntinus*) is another such species that persisted in Eurasia until the Mid-Late Holocene. Yet, unlike other widespread Pleistocene species it is one of the most poorly understood despite surviving until relatively recently. This is partly due to the relatively small number of fossil records in comparison to other Late Quaternary megafaunal mammals, but also due to taxonomic confusion that is still being resolved. Yet as another now-extinct

survivor of the Pleistocene-Holocene transition, this species could yield further insights into end-Pleistocene megafaunal extinction dynamics and the nature of faunal response to climatic and anthropogenic impacts.

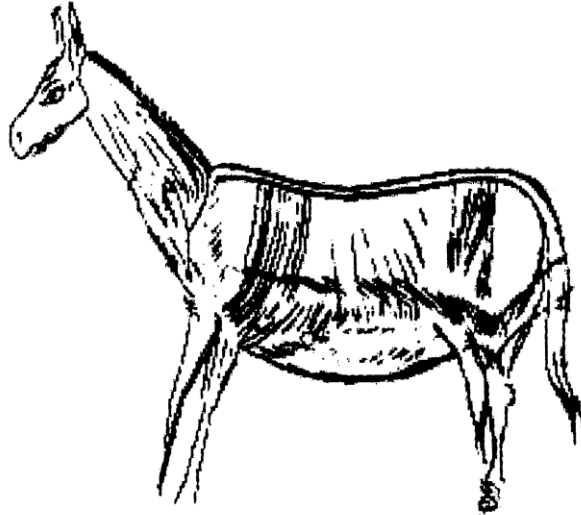


Figure 4.1 An Upper Palaeolithic cave painting of *E. hydruntinus* from the “Trois Frères cave” in France, drawn by H. Brueil. Taken from Antunes (2006).

E. hydruntinus was first described by Regalia (1907) based on bone fragments found in southern Italy, and was then studied by Stehlin and Graziosi (1935) based on fossils from the Upper Palaeolithic Romanelli cave in the same region of Italy. These authors compared the anatomy of asses and hemiones and argued that the Romanelli fossils displayed a mixture of characteristics from both. More recently Burke *et al.* (2003) also confirmed that it shares morphological traits with numerous Old World Pleistocene equids, apart from horses; for example, it has limb bone proportions most similar to those of hemiones and its upper teeth more like the asses, whilst its lower teeth are more similar to *E. stenonis*. *E. hydruntinus* is generally characterised by small teeth, upper cheek teeth with small protocones, lower cheek teeth with a double asinine loop, a long buccal groove on the molars, and slender limb bones (Eisenmann and Patou 1980; Burke *et al.* 2003).

It has since been argued on both morphometric (Burke *et al.* 2003) and genetic (Orlando *et al.* 2006) grounds that *E. hydruntinus* was most closely related to hemiones. Burke *et al.* (2003) considered it to be a distinct species whereas subsequent molecular analyses have argued that it was probably a subspecies of *E. hemionus* (Orlando *et al.* 2009; Geigl and Grange 2012). However, Orlando *et al.* (2009) also noted that the kiang (*E. kiang*) and onager/kulan (*E. hemionus*) are currently classified as separate species on the basis of comparable levels of mitochondrial differentiation, and that the available genetic data therefore still allow for *E. hydruntinus* to be a separate species. However they suggest that this should be clarified with further information from nuclear loci.

E. hydruntinus was widespread across western Eurasia during the Late Pleistocene, with a geographic distribution from western Europe to the Volga, Turkey and the Middle East (Uerpmann 1987, Willms 1989; fig 4.2). This distribution was broadly congruent across this region with other large Pleistocene megafauna including cave lion *Panthera spelaea* (Stuart and Lister 2010), cave bear *Ursus spelaeus* (Pacher and Stuart 2008), giant deer (Stuart *et al.* 2004) and mammoth (Stuart *et al.* 2002) most of which required open landscapes that predominated across Eurasia during the Late Pleistocene (Ray and Adams 2001). The earliest fossil finds of *E. hydruntinus* were from contexts dated to around 350,000 years ago, such as Lunel-Viel in France (Bonifay 1991). Its Holocene range has up until now only been described for specific localities and regions, and Holocene spatial and temporal distribution data have not been synthesised. Therefore, the spatial response of *E. hydruntinus* to end-Pleistocene climate change has not been assessed, nor the correlates of its Holocene range or subsequent extinction. Antunes (2006) suggested that *E. hydruntinus* may have even survived into the thirteenth century in Portugal and the sixteenth century in southeastern Spain. He argued that the mediaeval word 'zebro' corresponded to *E. hydruntinus*, and was mentioned in Forais (mediaeval charters) and used as the basis of numerous toponyms in Portugal. Moreover the zebro was described in some detail as resembling a wild ass. He suggested that *E. hydruntinus* finally became extinct thorough increased human pressure and deforestation. A closer examination of the available Holocene data may therefore contribute towards a better understanding of the distribution and range decline of *E. hydruntinus* that ultimately led to its global extinction, and to assess whether these patterns are congruent with wider faunal dynamics shown by other components of the western Eurasian mammalian megafauna during the Late Quaternary.

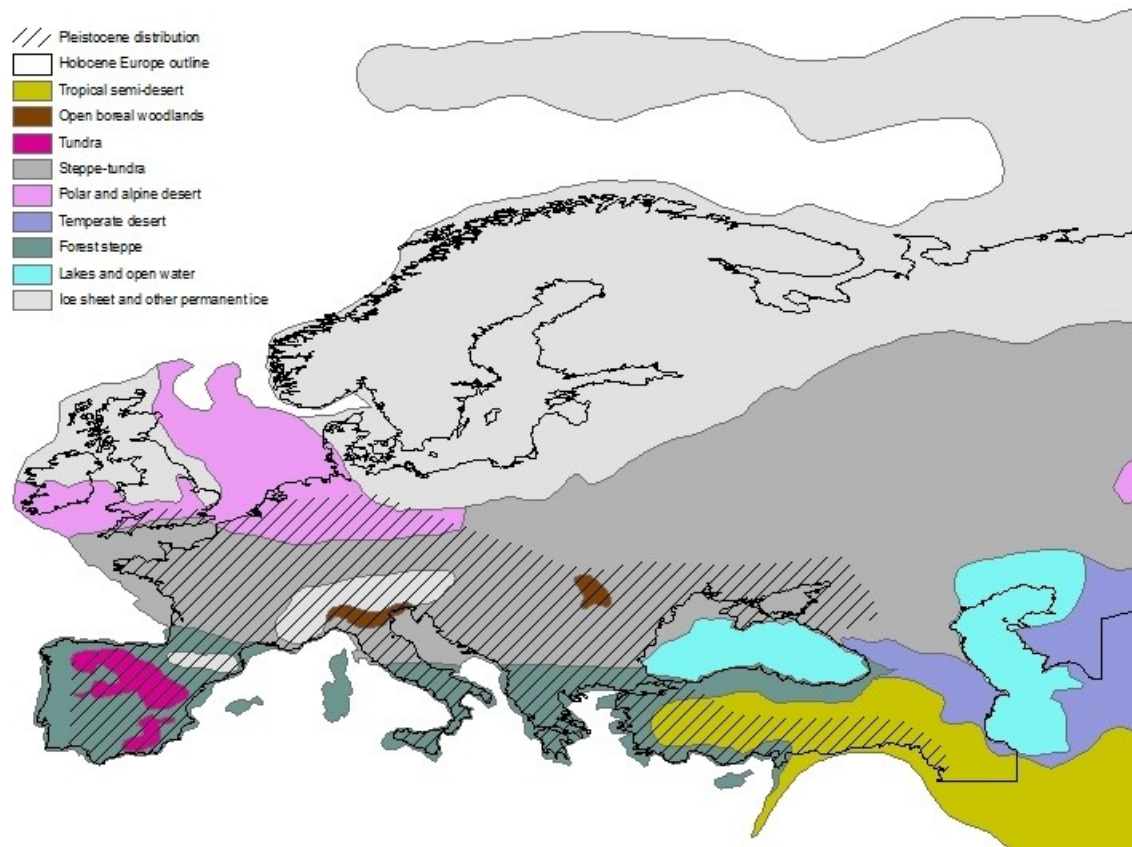


Figure. 4.2 Maximum extent of *E. hydruntinus* during the Pleistocene in Europe and major Late Glacial Maximum (LGM) biomes (modified from Ray and Adam 2001).

4.3 Methods

4.3.1 Data collection

All Holocene records of *E. hydruntinus* that could be located were sourced from the literature, including both journal articles and grey literature (see Chapter 2). Unpublished data from Armenia was obtained from the Institute of Zoology in Yerevan (Ninna Manaserian, Institute of Zoology, Armenian National Academy of Sciences, personal communication, April 2011) during fieldwork in the Caucasus. Additional zooarchaeological records from Iran were also included as a Late Holocene occurrence that was recently discovered but represents the only Holocene occurrence outside Europe. Records of *E. hemionus* from southeastern Europe were also compiled to investigate whether the two taxa were allopatric or sympatric across any parts of their respective ranges. If the two equid species did overlap in range, then zooarchaeological identification must be undertaken carefully in these regions and, where identifications appear uncertain, records treated with caution. Information was compiled on each geographical location to as accurate a degree as possible. Where records were not already fully georeferenced in the literature, the name and/or location of the zooarchaeological or subfossil site was searched for in a georeferencing facility such as iTouch

(<http://itouchmap.com/latlong.html>). See Chapter 2 for a fuller account of data collection methods and dating protocols. All final date intervals were then plotted according to region in order to illustrate the persistence of the species across different areas of its range. See Appendix 4 for a list of references for all zooarchaeological records for *E. hydruntinus* and *E. hemionus*.

4.3.2 Spatial analysis

Point pattern analysis was carried out to investigate the spatial spread of the data and to analyse levels of fragmentation of the Holocene distribution of *E. hydruntinus*. Point pattern analysis is widely used in spatial analyses, for example in epidemiology and increasingly in ecology, to study population distributions of species. A point pattern comprises a set of point locations, usually spatial coordinates, within a specific study area (Lloyd 2010). Basic visual inspection of any point pattern is the first sensible step and will usually give general impressions of any obvious patterns that are inherent in the distribution. However, estimating measures that can quantify certain aspects of the point pattern can further inform the analysis, particularly for complex patterns, and can ultimately help to identify the underlying processes driving the distribution. There are two main approaches to describing point patterns, which describe either first-order or second-order properties.

First-order properties are concerned with the intensity of the point pattern, or point density, and generally describe how events are distributed in space. I used a fixed-bandwidth kernel density estimate within the R package *spatstat*, within the statistical programme R Studio, version 0.94.105 (RStudio 2012), to investigate the spread and intensity of points across the sampled region, based on the confirmed records of *E. hydruntinus*. This kernel density function provides an estimate of the intensity function of the point process that generated the point data, and can be used to extrapolate an approximation of geographical range based on location data. Density maps can then be produced to visually represent variations in intensity of occupation of different areas and therefore the spatial distribution of a species across a landscape (Bivand *et al.* 2008).

Second-order properties are concerned with the spatial spread of the points, or point separation, and tend to examine the existence of possible interactions between points. A tight grouping of points for example could reflect high intensity, or clustered events. I used a simple aggregation index, the Clark Evans index, to statistically investigate clustering or ordering of the point pattern. This index provides the ratio of the observed mean nearest neighbour distance in the pattern to that expected for a Poisson point process of the same intensity (Clark and Evans 1954). A value of $R > 1$ suggests ordering, while $R < 1$ suggests clustering. This analysis was also carried out in R Studio (RStudio 2012). These methods allowed me to firstly, estimate the approximate distribution of *E. hydruntinus* based on relatively few sampling points, and secondly, analyse the degree of clustering of the data to indicate levels of range fragmentation.

Finally, the most up-to-date available vegetation maps for the Early Holocene at 8000 BP and the Late Holocene at 1000 BP (simulated by Kleinen *et al.* 2011) were digitised using ArcMap 9.3 (ESRI

2008) to identify environmental correlates that might have been driving the Holocene distribution of *E. hydruntinus*. GIS layers for elevation and Europe's rivers were also used to investigate any topographical features that may have shaped its distribution.

4.3.3 Temporal analysis

Optimal linear estimation (OLE) was carried out to model a global extinction date for *E. hydruntinus*. This is a method used to estimate extinction dates based on last occurrence sighting records (Solow 2005). It is a probabilistic approach that uses the temporal distribution of independent, uncorrected sighting events to estimate an extinction date based on the Weibull distribution (Crawley 2007). The method has predominantly been used on sightings and recent historical records (Solow 2005; Turvey et al. 2010), but has also been used on natural history collections (Solow and Roberts 2003) and on the Late Pleistocene fossil record (Solow *et al.* 2006). It assumes that sighting effort, whilst potentially variable, never falls to zero (Collen and Turvey 2009). Whilst the zooarchaeological record is not precisely analogous to ecological sampling techniques, the extensive and rich zooarchaeological record of Europe arguably reflects an intensive and consistent sampling effort of faunal assemblages over time. The analysis was carried out following Solow (2005) using the midpoint of each time interval used as the 'sighting date' for each record in R Studio (RStudio 2012).

4.4 Results

4.4.1 Holocene distribution of *E. hydruntinus*

Sixty six occurrences of *E. hydruntinus* were compiled from Holocene Europe (Table 1; Appendix 4). All records originated from archaeological deposits. Nine records were associated with a stratigraphic radiocarbon date, thirty-one were associated with a specific culture and all others were dated according to archaeological periods. The overall number of records was relatively low when compared with other European ungulates that had a Holocene distribution across a large part of Europe (see Chapter 2, fig. 2.3). There was some spatial overlap between the *E. hydruntinus* and *E. hemionus* (fig. 4.3). This provides a note of caution with regards to distinguishing between these two closely similar species in the recent zooarchaeological record; indeed it may be that some finds in the geographical region of overlap are worthy of further investigation to verify their accurate species-level identification.

Table 4.1 Holocene records of *E. hydruntinus* and *E. hemionus* from Europe

Country	Site	Date	Associated culture	Context dates (¹⁴ C, as reported)	Assigned date (years BC)	Reference
Confirmed <i>E. hydruntinus</i> records:						
Armenia	Adablur	Mid 4th mill BC			3500	C. K. Mejlumian 1988
Armenia	Keti	End 2nd - beginning 1st mill. BC			1500-500	C. K. Mejlumian 1988
Armenia	Khatunarkh	5th and beginning 4th mill. BC			5000-3500	C. K. Mejlumian 1988
Armenia	Mokhrablur	First half and mid 3rd mill. BC			3000-2500	C. K. Mejlumian 1988
Armenia	Shengavit	End 4th-3rd mill. BC			3500-2000	C. K. Mejlumian 1988
Armenia	Teghut	First half 4th mill. BC			4000-3500	C. K. Mejlumian 1988
Austria	Donnerskirchen	Early Neolithic, Atlantic period			5000-4250	Pucher 1991
Austria	Schleinbach	Late Neolithic	Epi-Lengyel		4200-3750	Pucher 1996
Bulgaria	Durankulak		Karanovo VI	5645±87 BP	4600-4200	Nobis 1986b
Bulgaria	Durankulak	Eneolithic			3900-3400	Manhart 1998 in Ninov 1999
Bulgaria	Karanovo		Karanovo I		6450-3750	Bökönyi & Bartosiewicz 1997
Bulgaria	Karanovo		Karanovo II		6450-3750	Bökönyi & Bartosiewicz 1997
Bulgaria	Karanovo		Karanovo VII		3300-2700	Bökönyi & Bartosiewicz 1997
Bulgaria	Ovčarovo-gorata	Early Neolithic	Karanovo II		6200-5500	Nobis 1986a
Bulgaria	Ovčarovo-gorata	Eneolithic			4600-4200	Vasilev 1983 in Ninov 1999
Bulgaria	Pomoštica	Neolithic			6000-4500	Ninov 1999
Czech Republic	Chotěbudice	Neolithic			5000-3500	Peske 1989a in Kysely 2005
Czech Republic	Jelení louka	Neolithic			5000-3500	Kratochvil 1973 in Kysely 2005
Czech Republic	Těšetice-Kyjovice	Neolithic			5000-3500	Dreslerova in press [2006], in Kysely 2005
France	Gramari (Methamis)	Mesolithic	Sauveterrien		8500-6500	Poulain 1971
France	Grotte de Felines-Termenès	Mesolithic?			9000-5000	Eisenman and Patou 1980
France	Vallerauge (Gard)	Mesolithic			9000-5000	Ducos unpubl. in Uerpmann 1976
Hungary	Aba-Felsőszentiván	Middle Neolithic	Linear Pottery		5260-4880	Vörös 1981
Hungary	Balatonkeresztúr	Mesolithic			9000-6000	Vörös 1981
Hungary	Endrőd	Early Neolithic	Körös		6000-5500	Bökönyi 1992
Hungary	Gyalaret-Szilagy	Early Neolithic	Körös-Starčevo	7090±100 BP	6207-5746	Vörös 1981
Hungary	Hódmezővásárhely-Bodzáspart	Early Neolithic	Körös-Starčevo		6400-5500	Vörös 1981
Hungary	Kecel-Tőzegtelep	Mesolithic			9000-6000	Vörös 1981
Hungary	Lebő	Late Neolithic	Tisza		4800-3500	Vörös 1981
Hungary	Mezőlak-Tőzegtelep	Mesolithic			9000-6000	Vörös 1981
Hungary	Röszke-Lúdvár	Early Neolithic	Körös-Starčevo		6400-3500	Vörös 1981
Hungary	Szabadszállás-Tőzegtelep	Mesolithic			9000-6000	Vörös 1981

Hungary	Szajol-Felsőföld	Early Neolithic	Körös-Starčevo		6400-3500	Vörös 1981
Hungary	Szegvár-Tűzköves	Late Neolithic	Tisza		4800-3500	Vörös 1981
Iran	Qabrestan	Chalcolithic		3782-3102 cal. BC	3782-3361	Mashkour <i>et al.</i> 1999
Iran	Sagsabad	Iron Age		1294-863 cal. BC	1294-1035	Mashkour <i>et al.</i> 1999
Iran	Zagheh	Neolithic		5212-4561 cal. BC	5212-4918	Bocherens <i>et al.</i> 2000
Italy	Grotta della Mura	Mesolithic/Late Neolithic		8240±120 BP; 8290±50 BP	7490-7178	Bon & Boscato 1993; 1995
Italy	Rendina, Basilicate	Early Neolithic			6000-5000	Bökönyi 1982 in Wilkens 1999
Italy	Terragne	Early Neolithic			6000-5000	Di Lernia 1996 in Wilkens 1999
Romania	Ceamurlia de Jos	Neolithic	Hamangia		5250-4500	Samson & Radalescu 1966
Romania	Cernavoda	Early Neolithic	Hamangia		5250-4500	Necrasov & Haimovici 1959
Romania	Cheia	Neolithic	Hamangia		5250-4500	Balalsescu & Radu 2003 in Haimovici & Balalsescu 2006
Romania	Golovita	Neolithic	Hamangia		5250-4500	Samson & Radalescu 1966
Romania	Gornea-Căunița de Sus	Neolithic	Starčevo-Criș		6400-5500	El Susa-Georgeta 1985 in Haimovici & Balalsescu 2006
Romania	La Adam	Mesolithic and Neolithic aceramic			8000-5000	Samson and Radalescu 1966
Romania	Limanu	Neolithic	Hamangia		5250-4500	Samson and Radalescu 1966
Romania	Ostrovul Corbului	Mesolithic	Schela Cladovei		7061-6439	Haimovici 1987
Romania	Techirghiol	Neolithic	Hamangia		5250-4500	Samson & Radalescu 1966; Haimovici & Balalsescu 2006
Serbia	Csoka	Late Neolithic	Tisza		4800-3500	Vörös 1981
Serbia	Lepenski Vir	Early Neolithic	Körös-Starčevo		6400-5500	Vörös 1981
Serbia	Ludas	Early Neolithic	Körös-Starčevo		6400-5500	Vörös 1981
Serbia	Nosza Gyöngypart	Neolithic	Criș		6400-5500	Samson & Radalescu 1966, Vörös 1981
Spain	Cueva de la Carigüela	Early Neolithic		7010±90 BP	5500-4750	Uerpmann 1976
Spain	Terrera Ventura	Chalcolithic	Los Millares		3200-2500	von den Driesch 1972
Turkey	Asikli Hoyuk	Early Neolithic			8040-7490	Buitenhuis <i>et al.</i> 1999
Turkey	Can Hasan III	Neolithic, late 7th/early 6th mill. BC			6500-5000	Uerpmann 1987; Payne 1991
Turkey	Çatal Hüyük	Neolithic		7300-6200 cal. BC	7300-6200	Russell & Martin 2005
Turkey	Pınarbaşı			9290±80 BP, 9140±80, BP 9050±80 BP	8726-8306	Carruthers 2004a
Turkey	Pınarbaşı			5725±65 BP, 7145±70 BP, 4550±70 BP	4724-4402	Carruthers 2004b
Ukraine	Mirmoe	Late Mesolithic	Grebenikov		6500-5500	Benecke 1998
Ukraine	Șan-Koba	Early Mesolithic			9000-7000	Benecke 1999a
Ukraine	Seliste	Neolithic			5000-2750	David 1977 in Bonifay 1991
Ukraine	Semenovka I		Surskaya		6550-5200	Kotova 2003
Ukraine	Semenovka I		Azonovo-Dnieprovskaya		5200-4750	Kotova 2003
Ukraine	Sjuren' II	Early Mesolithic			9000-7000	Benecke 1999a

Questionable *E. hydruntinus* records:

Georgia	Didi-gora	Middle Bronze Age		2300-1600 BC		Uerpmann & Uerpmann 2008
Georgia	Didi-gora	Iron Age		1075 cal. BC		Uerpmann & Uerpmann 2008

Georgia	Tqisbolo-gora		1800-800 cal. BC	Uerpmann & Uerpmann 2008
Spain	Cueva del Moro	Early Neolithic		Castaños Ugarte 1991
Turkey	Demirci Hüyük	Bronze Age		Uerpmann 1987
Turkey	Karataş-Semayük	Bronze Age		Uerpmann 1987
Turkey	Sös Höyük	Early Bronze Age		Howell-Meurs 2001

E. hemionus records:

Armenia	Ayrivan	2nd mill. BC		C. K. Mejlumian 1988
Armenia	Benjamin	6th century BC - 4th century AD		N. Manaserian 2011
Armenia	Metsamor	Neolithic, last half 18th century AD		N. Manaserian 2011
Armenia	Mokhrablur	First quarter 4th & first half 3rd mill. BC		N. Manaserian 2011
Armenia	Sevan	End 3rd & first half 2nd mill. BC		C. K. Mejlumian 1988
Armenia	Shengavit	Early Bronze Age, end 4th-3rd mill. BC		N. Manaserian 2011
Armenia	Teyshebaini	9th-8th century BC	Urartu	N. Manaserian 2011
Armenia	Tsamakaberd	Late Bronze Age, 2nd-1st mill. BC		C. K. Mejlumian 1988
Azerbaijan	Baku fortress	13th century AD		Vereshchagin 1959
Georgia	Edzani (Barmaksiz)	Mesolithic?		Bendukidze 1979
Georgia	Imiris-Gora	5th-4th mill. BC		Bendukidze 1979
Georgia	Udabno I	Iron Age		Uerpmann 2006
Georgia*	Zurkateti	Mesolithic?		Bendukidze 1979
Rostov Oblast	Sarkel fortress	9th - 13th centuries		Vereshchagin 1959
Russia	Kayakent/Dzhemikent	Bronze Age, second half of 2nd mill. BC		Vereshchagin 1959
Russia	Sunzha valley	2nd -3rd centuries AD		Vereshchagin 1959
Turkey	Büyüktepe Höyük	Iron Age		Howell-Meurs 2001
Turkey	Çatal Hüyük	Neolithic	7300-6200 cal. BC	Russell & Martin 2005
Turkey	Çayönü Tepesi	Early Neolithic		Uerpmann 1987
Turkey	Göbekli Tepe		9559±53 BP, 9452±73 BP	Peters & Schmidt 2004
Turkey	Gritille	3rd mill. BC		Stein 1987
Turkey	Nevalı Cori	Pre-Pottery Neolithic	9280±55, 8610±90 BP	Grupe & Peters 2008
Turkey	Pınarbaşı		5725±65 BP, 7145±70 BP, 4550±70 BP	Carruthers 2004b
Turkey	Saraiulakh		4000-2000 BP	Vereshchagin 1959
Turkey	Tilbesar	Middle Bronze Age		Berthon & Mashkour 1998
Turkey	Titris Hoyuk	Early Bronze Age		Greenfield 2002
Ukraine	Sobachki		6050-4750 BC	Kotova 2003
Ukraine	Surskii Ostrov	Early Neolithic		Burchak-Abramovich 1980

* *E. cf. hemionus*

4.4.2 Spatial analysis

Kernel density estimation (fig. 4.4) provided an estimated Holocene distribution of *E. hydruntinus* over Europe. The intensity of points was concentrated in central Europe, with slightly patchier areas in Turkey, the Caucasus and Iran. Minor areas of range were also indicated for southern Spain, southern France and southern Italy. However, there were large areas of zero density between these clusters that indicated an overall non-contiguous, fragmented distribution which was confirmed as statistically highly clustered (Clark Evans test, $R = 0.269$, $p < 0.001$).

The Late Pleistocene distribution of *E. hydruntinus* was substantially larger than its Holocene distribution and followed areas of open-vegetation biomes, mostly tundra, steppe-tundra and forest-steppe, right up to the southern edge of the Late Quaternary ice sheet (fig. 4.2). Likewise during the Holocene, its distribution was predominantly restricted to open landscape (fig. 4.5) but these areas now comprised a far smaller proportion of the landscape and were mostly restricted to southern Europe. Whilst not all areas of open landscape contained records of *E. hydruntinus* evenly throughout the habitat, there were few tree-covered areas that did contain records of *E. hydruntinus*, apart from in the Czech Republic and Austria. However, records from central and eastern Europe also closely followed the length of the Danube valley from Austria to the Romanian-Ukrainian border, apart from the one record from northern Czech Republic (fig 4.3). By the Late Holocene, the open vegetation in central Europe had been replaced by tree cover and there were no further *E. hydruntinus* records from this region (fig. 4.5).

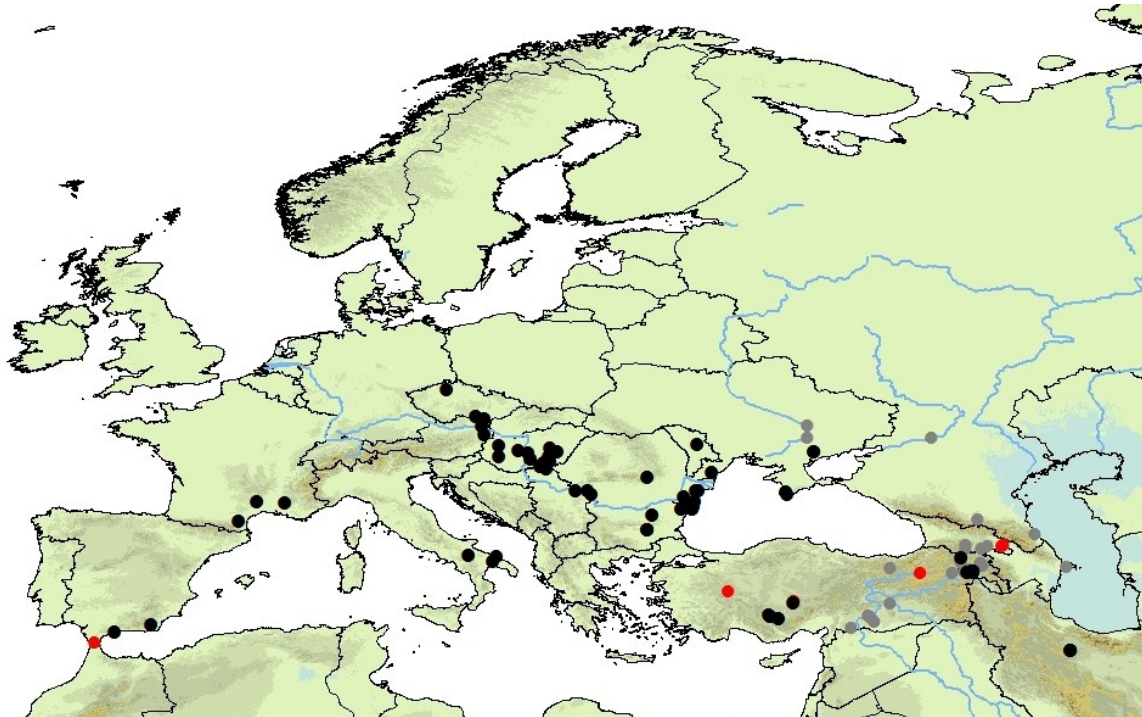


Figure 4.3 Holocene distribution of *E. hydruntinus* and *E. hemionus*, showing confirmed finds for *E. hydruntinus* (black circles), *E. hemionus* records (grey circles) and questionable *E. hydruntinus* records (red circles): the record in Spain was possibly domestic ass due to mixing of archaeological layers, and those in Turkey and the Caucasus could have been *E. hemionus*.

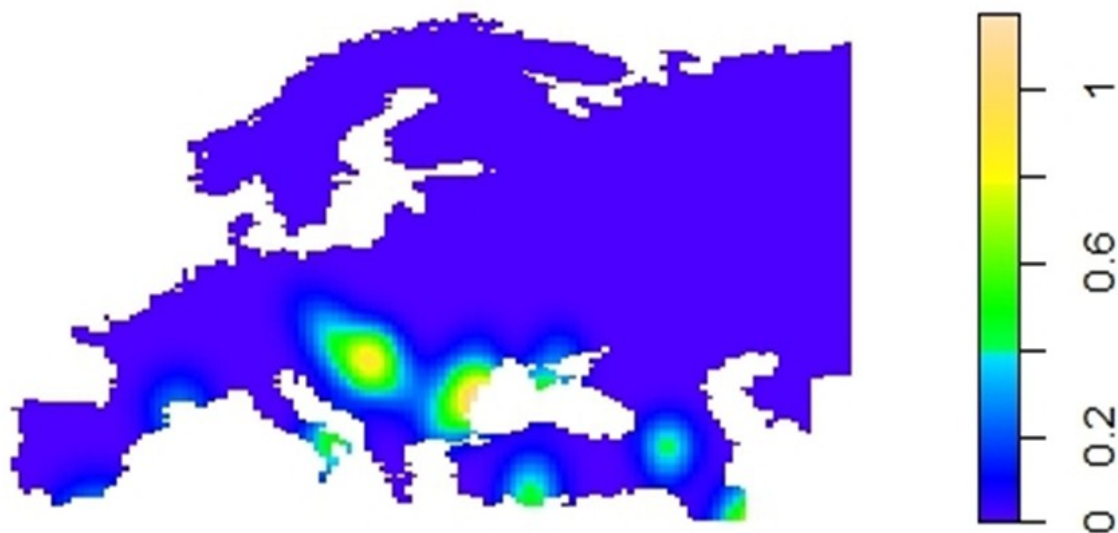


Figure 4.4 Output of the kernel density estimation model for the Holocene distribution of *E. hydruntinus*

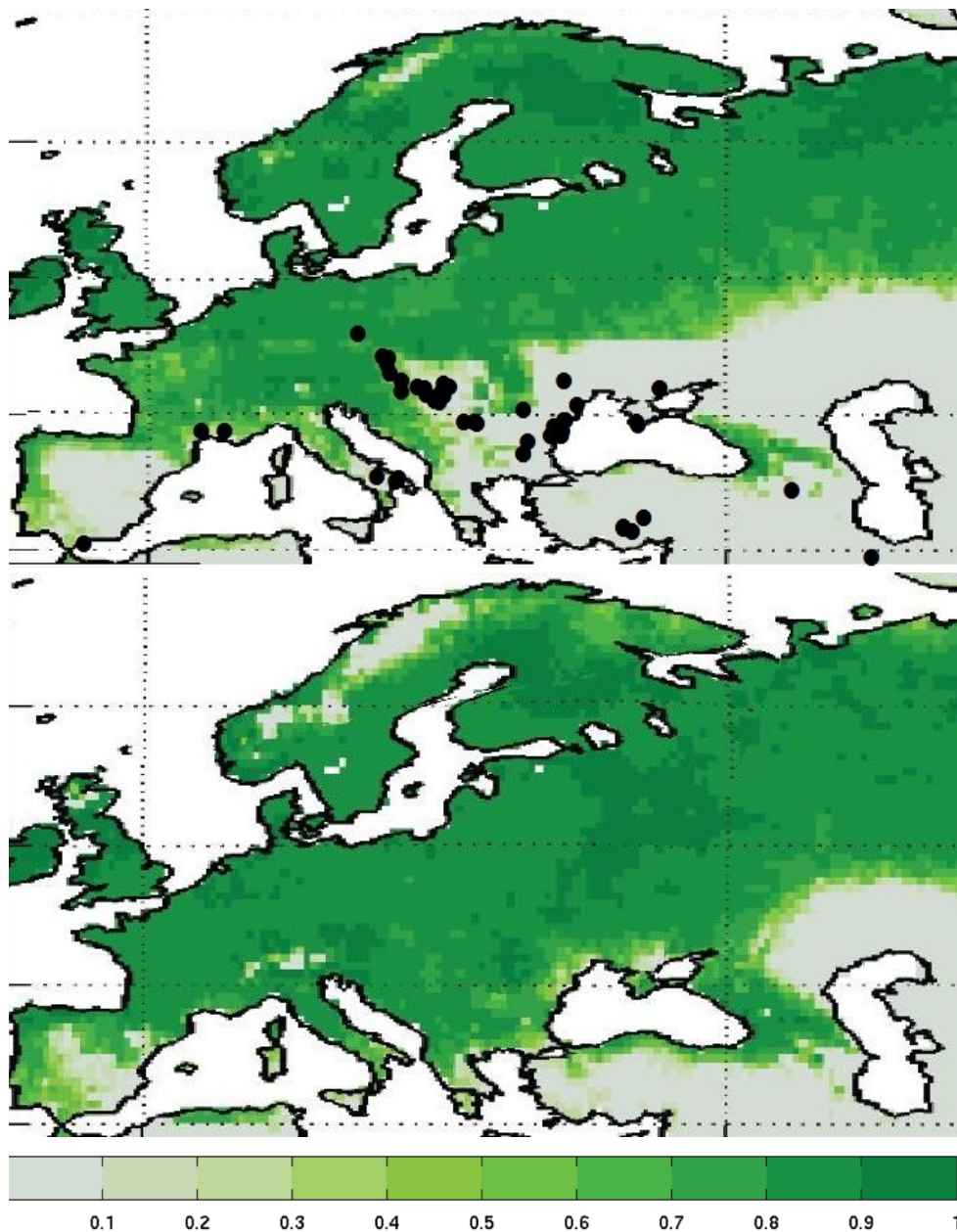


Figure 4.5 Simulations of model-predicted tree cover (Kleinen *et al.* 2011) at 8 ka BP (top) with *E. hydruntinus* distribution at the corresponding Early-Mid Holocene (black circles); and at 1 ka BP (bottom).

4.4.3 Temporal distribution of the data

During the Holocene *E. hydruntinus* finds ranged temporally from the Mesolithic to the Bronze Age in Europe and to the Iron Age in Iran and the Caucasus (fig. 4.6). In the Mesolithic and early Neolithic, *E. hydruntinus* was distributed in southern France and Italy. The central part of the range ran through Hungary, Serbia, Romania and Bulgaria and over the northern Black Sea coast into southern Ukraine. The eastern part of the range was in central-western Anatolia with two possible records further east into the Caucasus. By the Neolithic it had disappeared from southern France but there were still some records in southern Spain and Italy; it was still distributed in

central and eastern Europe, and there were also records from the Caucasus and northern Iran. By the Bronze Age zooarchaeological evidence was restricted to southwest Asia (Turkey, the southern Caucasus and Iran). The Iron Age has produced the most recent finds of *E. hydruntinus*, from Iran and Armenia. There was also thought to be an *E. hydruntinus* specimen from Cerro de la Virgen in Spain that was originally assigned to the Chalcolithic; however this was subsequently radiocarbon dated to the Middle Ages at 1170 ± 20 BP and re-identified as mule (von den Driesch 2000).

Optimal linear estimation returned an estimated extinction date for *E. hydruntinus* of 700 BC, with a lower confidence limit of 956 BC and an upper confidence limit of AD 346.

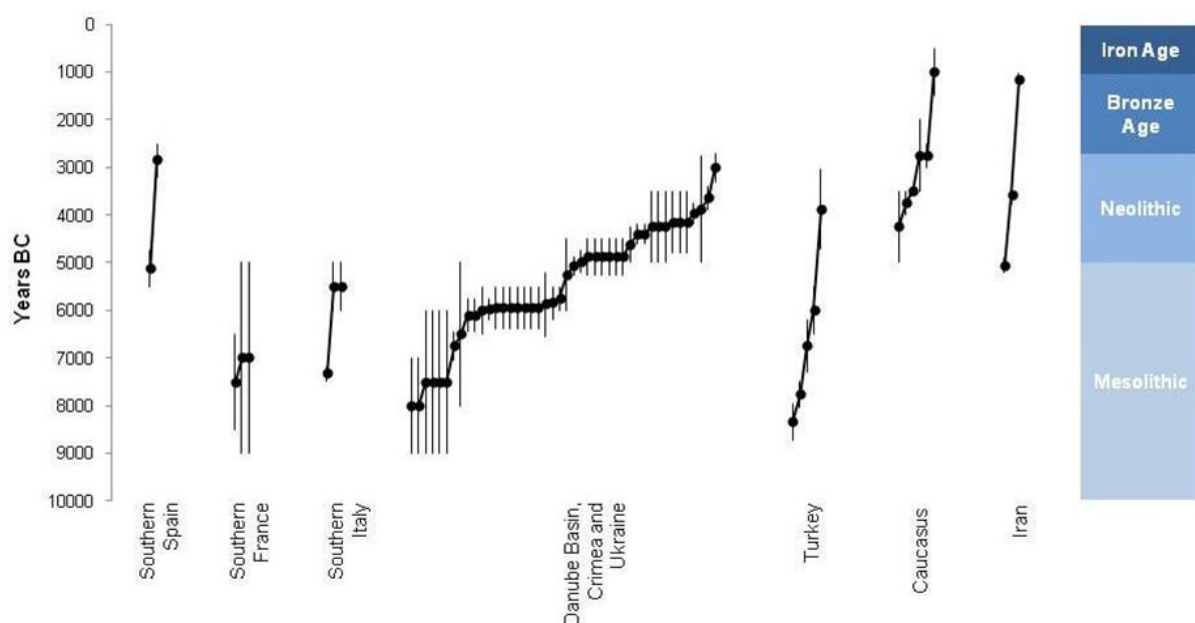


Figure 4.6 Temporal distribution of *E. hydruntinus* records across regions of Europe and southwest Asia. Each record is a bar representing its estimated date as a time interval with the midpoint of each as a black circle. Dates are shown both in calendar years (left) and in archaeological periods (right).

4.5 Discussion

4.5.1 Spatial extinction patterns

The overall small number of Holocene records for *E. hydruntinus* (Chapter 2, fig. 2.3) suggested that it was already a rare component of the fauna of Europe after the last Ice Age glaciation. As with any analysis based on fossil data, it is likely that there are more remains of *E. hydruntinus* yet to be found in Eurasia. Therefore it is difficult to make absolute statements on past distributions. The issue of whether the number of fossil records for a species reflects true ecological abundance is also a pervasive and problematic one for palaeobiologists (Turvey and Blackburn 2011) and this issue has been covered in more detail in Chapter 3. However, Europe is extremely well sampled archaeologically, so we can be fairly certain that this species was not as wide ranging or abundant as other European megafauna.

A lower abundance of *E. hydruntinus* compared to other mammal species in the European Holocene was also supported by its restricted distribution. At the end of the Pleistocene, *E. hydruntinus* was distributed from northern Europe, east as far as the Black Sea, in southwest Turkey and in southern Spain (fig. 4.2). This distribution was likely to have covered an even slightly larger extent given the lower sea levels during the Late Pleistocene; the species may have been distributed across the area now covered by the northern Adriatic Sea, and it may have been able to disperse more easily around major topographical barriers such as the Pyrenees and the Alps. An extended distribution beyond Holocene coastlines is partly corroborated by fossil metapodia and a phalanx dredged from the Brown Ridge under the North Sea between Britain and the Netherlands dating to the Middle-Late Pleistocene (Hooijer 1984; 1985). During the Late Pleistocene of Europe the predominant biomes were open vegetation, comprising mostly steppe-tundra and forest steppe (Ray and Adams 2001). During this time *E. hydruntinus* reached its maximum distribution, limited northwards only by the southern extent of the Last Glacial Maximum (LGM) ice sheet.

During the Holocene however, the zooarchaeological record indicated that *E. hydruntinus* was predominantly distributed in the south of Europe, with only one find north of the Danube (in the Czech Republic). Its range was highly fragmented, particularly in west and central Europe, with only small areas of occurrence in southern Spain, southern France and southern Italy (figs. 4.3; 4.4). Eastwards, its distribution was somewhat more continuous along the Danube river valley and into Ukraine, although this population did not appear to persist longer than the more isolated populations (fig 4.6). Severe range fragmentation was supported by statistically significant clustering in the spatial occurrence data for the species. The isolation of small numbers of records in southern Spain, France and Italy suggested that at the end of the Pleistocene its distribution shifted southwards and populations fragmented into these peninsular refugia. Meanwhile, populations further east in Europe remained connected along the Danube valley. It would be interesting to investigate whether evidence for isolated and fragmented populations was supported at the phylogeographic level from ancient DNA analysis.

Range fragmentation is recognised as an important component of species range decline preceding extinction (Wilcox and Murphy 1985; Fahrig 2002). For example, a survey of past and present extinctions highlighted that among birds, large frugivores and insectivores were the first groups to become extinct in small fragments, and poor dispersers were particularly affected by habitat fragmentation (McKinney 1997). The predominant extinction pattern for most of the Late Pleistocene Eurasian megaherbivores was range contraction into remnant and/or peripheral areas of their former range (MacPhee *et al.* 2002; Stuart *et al.* 2004), consistent with current biogeographic extinction theory (Channell and Lomolino 2000a, b). However, the extinction dynamics of *E. hydruntinus* potentially represent an entirely unique extinction trajectory, underpinned by range fragmentation, rather than whole-scale range contraction.

The Iberian, Italian and Balkan peninsulas have been well recognised as southern European refugia (Stewart *et al.* 2010). Sommer and Nadachowski (2006) also argued for a Carpathian refuge on the basis of genetic and fossil data. This was supported by the occurrence data for *E. hydruntinus* which indicated a fourth major area of distribution in the Carpathian region (fig. 4.3). The specific distribution in this region along the Danube valley is of particular interest as Stewart and Lister (2001) noted the presence of northern cryptic cave refugia existing in 'deeply incised valleys' that often retained their own microclimates. Although this theory has been predominantly espoused for warm-adapted fauna during glacial periods, the distribution of *E. hydruntinus* may provide some of the first evidence for such river valleys providing refuge in temperate periods. *E. hydruntinus* was also distributed in southern France during the Mesolithic. This region is not usually recognised as a 'classic' refugium, however Valdiosera *et al.* (2007) identified three novel haplotypes for brown bears (*Ursus arctos*) from samples taken from the southern French site of Mont Ventoux 4 which were dated to the mid-Holocene and which they argued formed a new post-LGM European lineage. This new monophyletic group was therefore positioned between the Iberian and Italian/Balkan clades and offered the intriguing possibility of the existence of a postglacial refugium there, now possibly further supported by the postglacial distribution of *E. hydruntinus*. There is even some evidence to support the idea of southwest Asia as a refugial area, as it has recently been demonstrated that three clades of the Eurasian shrew (*Crocidura suavolens*) evolved in a 'hotspot of refugia' in parts of Turkey and the Caucasus during Pleistocene glaciations (Dubey *et al.* 2006). Furthermore, it has also been proposed that Turkey may have acted as a Pleistocene refugium for plant diversity (Medail and Diadema 2009).

It is interesting, though perhaps unsurprising, that some of the final populations of *E. hydruntinus* might have been found in the Iberian peninsula, since this region has acted as a refugium across the Quaternary. It provided the final refuge for Neanderthal populations in the Late Pleistocene (Jiménez-Espejo *et al.* 2007) and is also now the sole region of Europe inhabited by the azure winged-magpie (*Cyanopica cooki*) after populations in central Europe were displaced during Pleistocene glaciations (Fok *et al.* 2002). In addition, palaeoecological evidence posits more open landscapes on the Iberian peninsula well into the Late Holocene which supports the possibility of regional survival of *E.*

hydruntinus over most other areas of its Holocene distribution which seem to have become reforested by the Late Holocene (fig. 4.5).

It therefore appears that *E. hydruntinus* retreated into southern European refugia during the Holocene period. The term 'refugium' has been used to describe a wide variety of climatic and environmental conditions across a range of temporal and spatial scales (Ashcroft 2010). However it was originally used to describe areas where species or populations survived during glacial conditions and the phenomenon of glacial refugia has therefore dominated the literature, whilst the characteristics of interglacial/postglacial refugia have been far less well explored (Bennett and Provan 2008).

Unfortunately little is known about the specific ecology or climatic tolerances of *E. hydruntinus*, but as it is now known to be closely related to hemionines, it has been hypothesised that it would have been adapted to open, dry steppe environments (Antunes 2006). This is also confirmed by the Late Pleistocene environment in which it was distributed (fig. 4.2). In eastern Europe, sites such as Mirnoe in southwestern Ukraine and Durankulak in Bulgaria contained remains of saiga antelope (*Saiga tatarica*) and great bustard (*Otis tarda*) in association with *E. hydruntinus*, supporting palaeoecological evidence that small areas of southern Europe retained open habitats (Spasov 2009). From a study on a related species, Warmuth *et al.* (2011) also argued that two open vegetation refugia in the eastern European steppes and in Iberia supported the persistence of larger wild horse populations in the Mid-Holocene than the rest of Europe which was forested.

During the Early Holocene, Europe was rapidly reforested (Huntley 1990, Peng *et al.* 1995). Local-scale vegetation patterns have been notoriously harder to reconstruct and in southern Europe in particular there is often poor agreement between climate-driven model simulations and pollen data (e.g. Prentice *et al.* 1998; Brewer *et al.* 2009). However, most biome reconstructions for the Mid-Holocene (at c. 6000 BP) largely concurred that most parts of Spain, southern Italy, the southern Balkans and the Black sea coast, Turkey and southwest Asia retained more open woodland vegetation than northern regions (Peng *et al.* 1995, Prentice *et al.* 1998; Brewer *et al.* 2009). The most up-to-date forest simulations for Europe for the Early-Mid Holocene (8000 BP) (Kleinen *et al.* 2011) in particular showed very close correlation between the distribution of *E. hydruntinus* and non-forested areas (fig. 4.5). The major area of disagreement between the outcome of the vegetation models and the raw pollen data within these studies appeared to be the extent to which more open vegetation was spread northwards into the Balkan/Carpathian peninsula. However, as aforementioned, this part of the distribution may have represented a riverine/valley microclimate which was not picked up by broad-scale climate models or pollen data, but which nonetheless provided a refugium for *E. hydruntinus*.

The fact that all Holocene records of *E. hydruntinus* originated from zooarchaeological deposits also demonstrates that the species was being directly exploited in some way by humans. More specific evidence including a burnt phalanx from Methamis (Poulain 1971) also suggested that the species

was being utilised for food. This provides further support for specific extinction drivers and the dynamics of the species' decline. With increasingly small, isolated populations in shrinking habitat restricted to southern refugia, the species would have been at greater risk from restricted gene flow and human exploitation, which could have pushed the species to extinction. This model of refugial populations pushed to extinction by anthropogenic threats has also been proposed for the extinction of giant deer in the early Holocene (Stuart *et al.* 2004). These authors noted that the Pleistocene distribution of this species was controlled by climate acting through vegetational changes, with its distribution expanding during warmer interglacial periods and contracting into refugia during colder glacial periods. Although this was a pattern common to many other megafaunal species during Late Quaternary glacial-interglacial cycles (Stuart 1999), the giant deer may have failed to re-expand its distribution during the Holocene due to the novel threat of human activity that had not existed in previous interglacial periods, and the dynamics of the final extinction of *E. hydruntinus* during the Holocene are likely to have been very similar.

4.5.2 Temporal extinction patterns

Antunes (2006) has suggested that the species may have survived into the medieval period on the Iberian peninsula, based on toponyms and interpretation of historical records. However, there was no zooarchaeological evidence to substantiate this claim of late survival here, as the youngest well-supported data from Spain originated from Chalcolithic contexts around five thousand years ago. Orlando *et al.* (2009) also used morphometrics and mitochondrial DNA to analyse a specimen from Portugal dated to the seventeenth century which was reported to be the last 'zebro', but this was found to be a donkey. Thus no evidence at all for *E. hydruntinus* has been found from Portugal, although this country does have a younger tradition of zooarchaeology (Simon Davis, Instituto Portugues de Arqueologia, personal communication, 13 October, 2011), and therefore the possibility of future finds cannot be discounted. Indeed, so-called 'Lazarus taxa', where a species reappears in the fossil record after it has been considered extinct, are a well-known phenomenon in palaeontology (Flessa and Jablonski 1983).

Geigl and Grange (2012) also found that there was a huge divergence in classification of specimens of *E. hydruntinus* from western Europe by even experienced archaeozoologists and palaeontologists, with many finds dated between c.35,000 – 6000 BP yielding caballine rather than hemione genetic sequences. This raises the possibility of an even earlier extinction in this region, and also highlights that the morphological variability of Quaternary caballine equids in this region has been severely underestimated. The zooarchaeological records presented here did not form part of Geigl and Grange's dataset (Eva Geigl, Institut Jacques Monod du CNRS, personal communication, 28 May 2013), but should also be urgently examined to check their taxonomic status.

OLE based on all known Holocene zooarchaeological finds indicated a global extinction date considerably earlier than the sixteenth century, at around 700 BC with a minimum extinction estimate of 956 BC and a maximum extinction estimate of AD 346. However, the wide confidence bands of this

estimate suggested that this may not be an ideal technique for faunal assemblages that have not all been radiocarbon dated. The minimum distance method, on which OLE is founded, is based on the Weibull extreme value distribution, which tends to assume negligible errors associated with dating of sighting records (Solow *et al.* 2006) and therefore this model is not technically correct in the presence of measurement error (A. Solow, Woods Hole Oceanographic Institution, personal communication, 27 July 2011). Whilst radiocarbon dating can statistically estimate dating error, relative methods of dating cannot. Thus the use of a 'midpoint' from relative dating of zooarchaeological records, for which the potential error varied with each record, is likely to have substantially increased the confidence interval of the extinction estimate. Current methods for estimating extinction dates may not therefore be entirely appropriate for relatively dated (prehistoric) faunal records; although many techniques exist, each has its benefits and limitations (Collen and Turvey 2009). This is also further impetus for obtaining all Holocene specimens of *E. hydruntinus* in order to subject them to radiocarbon dating. However, with regards to the extinction of *E. hydruntinus* in Spain, OLE nevertheless supports an earlier date than that suggested by Antunes (2006), with the last populations probably occurring far further east in Iran where the most recent evidence originated. Whilst according to the old adage, absence of evidence cannot be taken as evidence of absence, survival beyond the Chalcolithic in Spain was an unlikely possibility unless substantially younger subfossil evidence is found there.

4.5.3 The extinction of *E. hydruntinus* within the wider context of Late Quaternary extinctions

Research into Late Quaternary extinctions has tended to focus on Late Pleistocene extinctions and the current extinction crisis, on the basis that these two periods have experienced the most concentrated loss of species globally in recent times. However, an increasing body of recent fossil and zooarchaeological evidence, comprising newly discovered extinct species from across the globe, is steadily demonstrating that the Holocene also witnessed a substantial number of global mammal extinctions, currently numbering 255 (Turvey 2009c), many of which were megafaunal species. In Africa, the long-horned buffalo (*Pelorovis antiquus*) became extinct in eastern and southern Africa by about 12000 years ago but survived in North Africa until around 4000 years ago (Klein 1994) and in China the short-horned water buffalo (*Bubalus mephistopheles*) survived until the Bronze Age (Yang *et al.* 2008). Miller (1986) discussed evidence for elephants occurring from the 2nd millennium BC in northern Syria and possibly southern Turkey, although they appeared to have become extinct by the 8th-9th century BC.

Whilst many other large mammal species have survived globally to the modern day, Holocene Europe has also witnessed several continent-level extinctions, mostly from the southern and eastern regions. As well as the possibility of elephants at its southern fringes, the European lion (*Panthera leo*) became extinct around 2000 years ago, having survived as far north as Hungary (Vörös 1983), and there is evidence for the survival of leopard (*Panthera pardus*) until the Mid-Late Holocene (Sommer and Benecke 2006). The Caucasus is also an extremely biogeographically interesting area, comprising the region where Europe, Asia and African faunas have converged and overlapped in

recent prehistory. As such it had populations of lion, cheetah and tiger until the tenth century, thirteenth century and 1930s respectively (Vereshchagin 1959).

Moreover, the timing of the extinction of *E. hydruntinus* highlights that the phenomenon of 'Late Pleistocene extinctions' belies a far more complicated process. Mammoth and giant deer for example have both been found in Holocene sites dating to around 4000 years ago on Wrangel Island and just over 7000 years ago in western Siberia respectively (Stuart *et al.* 2004). The authors argued that these reflected the overall 'ragged nature' of end-Pleistocene extinctions whereby different species became extinct in different areas and at different times, with 'successive contractions in range'. *E. hydruntinus* therefore represents yet another species in a long line of temporally non-congruent Late Quaternary megafaunal extinction events in northern Eurasia, underlining the staggered temporal nature of this process in this region (Stuart 1999) that lasted well into the Holocene.

This process contrasts with Late Pleistocene megafaunal extinctions in North America for example, almost all of which had taken place by 10,000 years ago (Grayson 1989). Whilst in North America and northern Eurasia it is now agreed that a combination of climate change and hunting caused Late Pleistocene extinctions (e.g. Guthrie 2006; Pushkina and Raia 2007; Nogues-Bravo *et al.* 2008), it has been proposed that extinctions in North America were more rapid and temporally congruent due to the simultaneous threats of climate change and novel human activity. By contrast, northern Eurasian populations of megafauna had lived alongside humans (both *Homo sapiens* and pre-*sapiens* hominins) such that the interplay between human activity and climate change was more complex (Barnosky *et al.* 2004). Furthermore, the existence of climatic refugia in southern Europe and eastwards into Siberia where human population density was lower provided areas for populations of Eurasian megafauna to retreat, regions which were apparently lacking in North America.

Understanding the factors which caused the extinction of a species in historical or prehistoric time is also of more than merely anecdotal interest. Many extinct species have highly threatened extant relatives that require conservation attention. Globally, extant equids are a highly threatened family: of the three remaining extant hemione and ass species, two are listed in IUCN threat categories; the most closely related species, the Asiatic wild ass, is listed as Endangered and the African wild ass (*E. africanus*) is listed as Critically Endangered (Moehlman *et al.* 2008). This study highlights the vulnerability of equid species to rapid climatic and environmental change and confirms the threat to isolated populations exacerbated by anthropogenic impacts such as hunting and further habitat modification.

4.6 Conclusion

This study demonstrates that the once widespread Pleistocene ass (*E. hydruntinus*) was a rare element in the fauna of Holocene Europe. The available evidence suggests that it gradually

succumbed to a combination of climate-driven vegetation change and human exploitation from the end of the Pleistocene to the Late Holocene. There is currently no zooarchaeological evidence to support a purported late survival of *E. hydruntinus* on the Iberian peninsula, although this cannot altogether be ruled out. The spatial and temporal patterns of its extinction trajectory are unique and underline the complexity of the processes behind Late Quaternary extinctions at an individual species level. However, vital future work should involve all Holocene specimens of *E. hydruntinus* being subjected to both ancient DNA testing and radiocarbon dating in order that the true distribution and accurate extinction chronology for the species can be reconstructed. This study contributes towards understanding the role of refugia as well as the complex interplay between environmental change and human impacts on species persistence. This could have relevance for the conservation of extant equid species as well as for understanding the demise of their extinct relatives.

Chapter 5. Spatial and temporal patterns of large mammal range shifts in the Holocene zooarchaeological record of Europe

5.1 Abstract

Range collapse is an important measure of a species' trajectory towards extinction but the lack of robust data on past species distributions has limited our understanding of both the temporal and spatial patterns of range decline. Using a large database of zooarchaeological records, European large mammal ranges were reconstructed and quantified for seven different time periods throughout the Holocene. Sample size variation was controlled for by bootstrapping in order to identify range declines independent of sample size. Around half of all mammal ranges declined significantly between the Iron Age and Late Medieval periods. Levels of decline were significantly associated with trophic level, with herbivorous species experiencing more extreme declines. Range shifts predominantly occurred in a north-easterly direction, consistent with movement away from areas of high human densities and habitat modification. These results highlight that in large-scale terrestrial systems with long histories of human impacts, prehistoric baselines may be required to fully capture the dynamics of species extinction processes and that imposing shorter term perspectives can distort our understanding of both the patterns and drivers of extinction.

5.2 Introduction

Conservationists are increasingly focusing on extinction as a process rather than a single event with greater emphasis on the factors influencing localised extirpations, population declines and range collapses (Soulé 1983; Gilpin and Soulé 1986; Caughley 1994; Ceballos and Erlich 2002). Thus a principle aim of conservation biology has been to develop methods to characterise this process and to generate indicators to measure declines that lead to species extinctions (Butchart *et al.* 2010). For example, the dynamics of population decline have been well described, and as a result populations of many species are now closely monitored in order to detect and predict trends over time (e.g. Loh *et al.* 2005; Collen *et al.* 2009, 2011).

However other important features of the extinction process remain relatively poorly understood, in particular spatial characteristics of species distributions and how these change over time. Geographic range is a fundamental ecological characteristic (Brown 1995; Gaston 2003). All species occupy a restricted geographic range which can be determined by both biotic factors such as life history, ecological niche and abundance, and abiotic physical characteristics of the environment such as topography and climate. However, most of these factors are not static, and consequently neither are species ranges (MacArthur 1972), which will instead exhibit flexibility in response to resource availability, environmental change and the evolution of species traits. Therefore in order to develop a

better understanding of the spatial characteristics of extinction processes and their correlates, geographic range is likely to represent a fundamental factor for further research.

However, studies of range dynamics and patterns of range change over time have been limited due to a lack of detailed data on past species distributions. This is principally due to the fact that quantitative studies and surveys of populations of most vertebrate species have only begun in recent decades (Loh *et al.* 2005). Most work to-date has calculated the extent of recent range loss for large mammals on continent-wide scales (Ceballos and Erlich 2002; Morrison *et al.* 2007) but has been based solely on one snapshot of historical range and a species' current range. Lomolino and Channell (1995) went further in their series of papers and compared historical and extant geographic ranges for species across a variety of taxonomic groups in order to characterise common dynamics and patterns of recent range declines. These authors predicted that geographic ranges would contract first along the range periphery and then towards the centre, on the basis that population densities are expected to be lower and less stable on a species' range periphery than in the centre. However, their results demonstrated that rather than contracting from the periphery inwards ("demographic hypothesis"), contraction occurred across the range ("contagion hypothesis") with most species maintaining at least a portion of their peripheral range following range contraction (Lomolino and Channell 1998; Channell and Lomolino 2000a, b). Interestingly this pattern predominated irrespective of taxonomic group.

Of the few studies that have focused on spatial patterns of range contraction specifically for mammal species, similar results were obtained. For example Laliberte and Ripple (2004) compared historical and extant ranges of carnivores and ungulates in North America, and found that for 12 out of 17 species whose range contracted more than 20%, contractions occurred towards the edge of their historical range. However, they also found that large carnivores and ungulates experienced a greater loss of range and that some smaller species that were well-adapted to human presence actually expanded their ranges.

However, due to the large amount of data over wide spatial and temporal scales that is required to fully characterise changes in species' geographic ranges, such studies have been limited to comparisons between present-day species distributions and single historical maps, usually no older than AD 1500, thus offering no long-term temporal framework for understanding species declines. This also misses out on the potential effects of huge expansions in human population across the globe before this period (Goudie 2006). Indeed Laliberte and Ripple (2004) observed the drawbacks of their data set being based on only two snapshots of the process, and Channell and Lomolino (2000b) also noted that a more comprehensive understanding of dynamic biogeography would need to include the sequence or trajectory that each species' range underwent to reach its final distribution. Excluding past biogeographical data also has implications for wider macroecology, with the inclusion of historical data potentially altering conclusions based on modern data alone. For example, although small geographic range size has been proposed as a key predictor of extinction risk in mammals (Purvis *et al.* 2000b; Cardillo *et al.* 2008), it has since been demonstrated this can actually be a

circular predictor if historical depletion of a species has occurred in response to past human impacts (Fritz *et al.* 2009; Hanna and Cardillo 2013).

On a continent such as Europe which has a long history of human occupation (Roebroeks 2006) this bias in data availability/interpretation is particularly salient. Indeed, previous studies have failed to identify distinct patterns between historical and current European mammalian range maps which the authors attributed to the fact that a depauperate mammal fauna was probably already in place by the nineteenth century (Ceballos and Erlich 2002). Greuter (1994) also compared rates of plant extinction in the Mediterranean with other climatically analogous areas and found these to be lowest in the Mediterranean. He attributed this phenomenon to the region's more ancient history of human impacts, such that prehistoric extinctions of vulnerable species probably went undocumented, leaving only those more resilient today. Despite being a generally well-studied continent, mammalian extinctions have only been documented at a regional or species level in Europe and even then, only within a qualitative rather than quantitative spatial framework (e.g. Yalden 1999, Van Vuure 2005). Available scattered information on last occurrence dates indicates that the timing and patterns of local extirpations may have been temporally non-congruent and unique for each species, but this has not been investigated on a continent-wide scale.

Current evidence relating to Late Quaternary megafaunal extinctions in Eurasia suggests that extinction patterns were not temporally discrete, being both species-specific in trajectory and 'staggered' in time extending well into the current Holocene epoch. Thus relict populations of giant deer (*Megaloceros giganteus*) are known to have survived the Pleistocene-Holocene boundary in the Ural mountains, mammoth (*Mammuthus primigenius*) similarly persisted on Wrangel Island, musk ox (*Ovibos moschatus*) is known from the Taimyr peninsula until the Late Holocene and European ass (*Equus hydruntinus*) lasted well into the Holocene in southern refugia (MacPhee *et al.* 2002; Stuart *et al.* 2004; Lorenzen *et al.* 2012; see also Chapter 4). This is a pattern that differs between continents and it has been suggested that extinction patterns might be related to the history of co-occurrence (and therefore possible co-evolution) with human populations (Martin 1984).

Given the complexity of the emerging picture of mammalian range shifts in Europe's recent past, it is imperative that data that extends beyond even the recent historical period is used to track species range shifts in highly anthropogenically modified ecosystems such as those in Europe, in order to develop a fuller understanding of wider patterns of species range change at both a continental and a faunal level. Fortunately, improved access to museum records and sharing of zooarchaeological datasets has now made long-term species occurrence data available (see Chapter 2) in order to study these processes on a more detailed temporal scale. This chapter therefore uses the zooarchaeological record of Europe to reconstruct large mammal distributions over the entire Holocene Epoch (11,500 years ago to present) in order to investigate spatial and temporal dynamics and patterns of geographic range shifts.

5.3 Methods

The zooarchaeological record as described in Chapter 2 was used as the basis for this study. All records were assigned to the following archaeological period(s) within which they fell:

Mesolithic	10,000 – 5500 BC
Neolithic	5500 – 3000 BC
Bronze Age	3000 – 1000 BC
Iron Age	1000 BC – 0 BC/AD
Roman Age	0 BC/AD – AD 500
Early Medieval	AD 500 – 1000
Late Medieval	AD 1000 – 1500
Modern	AD 1500 – 2000

Whilst not of equal length, these time periods were most informative in terms of specific changes in human subsistence and technology, or large-scale demographic change, that are likely to have had a major impact on the persistence of wild mammal populations. Non-congruity of these time periods across Europe was in general most marked during the Mesolithic and Neolithic but more or less corresponded by the Bronze Age/Iron Age.

Methods for reconstructing ranges have been widely discussed (Gaston 1994; Brown *et al.* 1996; Gaston 1996; Fortin *et al.* 2005; Gaston and Fuller 2009) but with no common consensus on an absolute method that is appropriate across all types of data or analysis. The zooarchaeological record consists of presence-only data, unlike ecological sampling which can yield presence-absence data. A common method to look at range change in the fossil record is therefore extent of occurrence (EOO), or range extent (e.g. Lyons 2003, 2005). This is the area measured with a convex hull polygon that encloses all the points with no internal angle measuring more than 180° (IUCN 2001).

As EOO is determined by the outermost points, ranges constructed this way can be skewed by outliers. It also assumes constant occupation across the range, and cannot therefore detect range fragmentation or unoccupied sites. However, methods to detect occupied range within a species' extent of occurrence, i.e. area of occupancy (AOO), are dependent on sampling effort within the overall EOO (Gaston and Fuller 2009) and therefore are likely to be skewed when using zooarchaeological records as they would reflect the number and spatial location of sampling points. Data based on sampling points are also subject to spatial autocorrelation, where observations at nearby locations are more likely to share similar properties than by chance, a common problem in ecology (Fortin *et al.* 2005). In order to test this, sampling points were aggregated into grid squares at increasing spatial resolutions and tested for spatial autocorrelation. As spatial autocorrelation was detected at all resolutions, even very coarse, this method was deemed inappropriate for opportunistically collected zooarchaeological data. In addition, several studies have actually found

strong correlation between different range size measures (Quinn *et al.* 1996; Blackburn *et al.* 2004; Beck *et al.* 2006), and so using only one absolute measure of range size was considered suitable. Extent of occurrence (EOO) was therefore used to reconstruct ranges across all species at each time period.

Creating a minimum convex polygon requires a minimum of three sampling points, and calculating range shifts required these measurements to be available for multiple consecutive time periods. Fifteen species were sufficiently numerous within consecutive time periods to calculate range sizes and shifts. However six species, wolverine (*Gulo gulo*), Iberian lynx (*Lynx pardinus*), European mink (*Mustela lutreola*), European lion (*Panthera leo*), European leopard (*Panthera pardus*) and reindeer (*Rangifer tarandus*), did not have enough records for these calculations so they were excluded from bootstrapping calculations and assemblage-wide analyses. As an introduced species across most of Europe, fallow deer (*Dama dama*) was also excluded from analysis. However, records for all seven species are still presented. Non-zooarchaeological records, including historical records, figurines and rock art, were also available for lion and leopard and are presented alongside range maps but these data were not included in EOO calculations.

Range centroids were then used to measure the direction and distance of range shifts for all species between each consecutive pair of time periods. One way ANOVA was used to test for differences between time periods and pairwise comparisons were then performed using Tukey Honest Significant Difference (HSD) tests to identify which time period transitions were driving any difference in the direction of shifts between time periods. All spatial analyses were calculated in ESRI ArcMap version 9.3 (ESRI 2008) and all statistical analyses were performed in R Studio, version 0.94.105 (RStudio 2012).

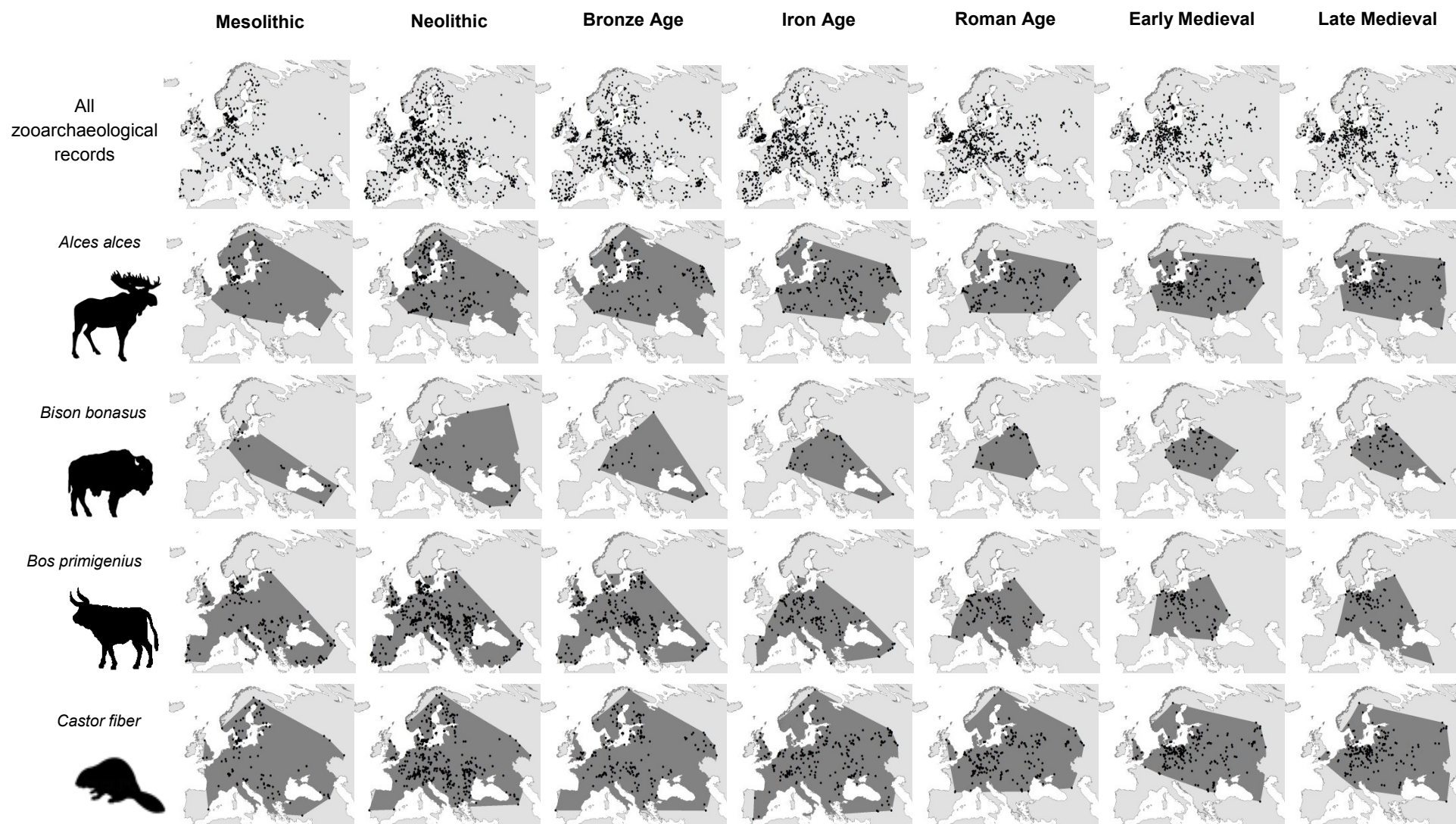
In calculating range sizes the number of zooarchaeological records and corresponding EOO were found to be positively correlated across all time periods and species. This was not surprising in itself and probably reflected the well-described positive abundance-occupancy relationship in ecology (Gaston 2000). However as a result of spatial, temporal and taxonomic variation in archaeological sampling (see Chapter 2; Chapter 3) it was difficult to separate the relative influence of the number of records and a genuine change in range from the observed EOO. Therefore an independent measure of the accuracy of observed range sizes was needed given the potentially confounding influence of sample size. Bootstrapping was therefore used to establish null models of range size expectations for each within-Holocene time period based on given sample sizes. This method 'resamples' the original data, with replacement, to estimate a statistic's sampling distribution and is therefore useful when the underlying sampling distribution cannot be assumed normal (Mooney and Duval 1993). For each species, all records across its Holocene range were randomly resampled 1000 times, with the sample size being the number of records for any one time period, and range size was calculated for each run. Upper and lower confidence intervals (95%) and mean range from the 1000 runs were then calculated and plotted together with the observed EOO. If the observed EOO fell outside these confidence

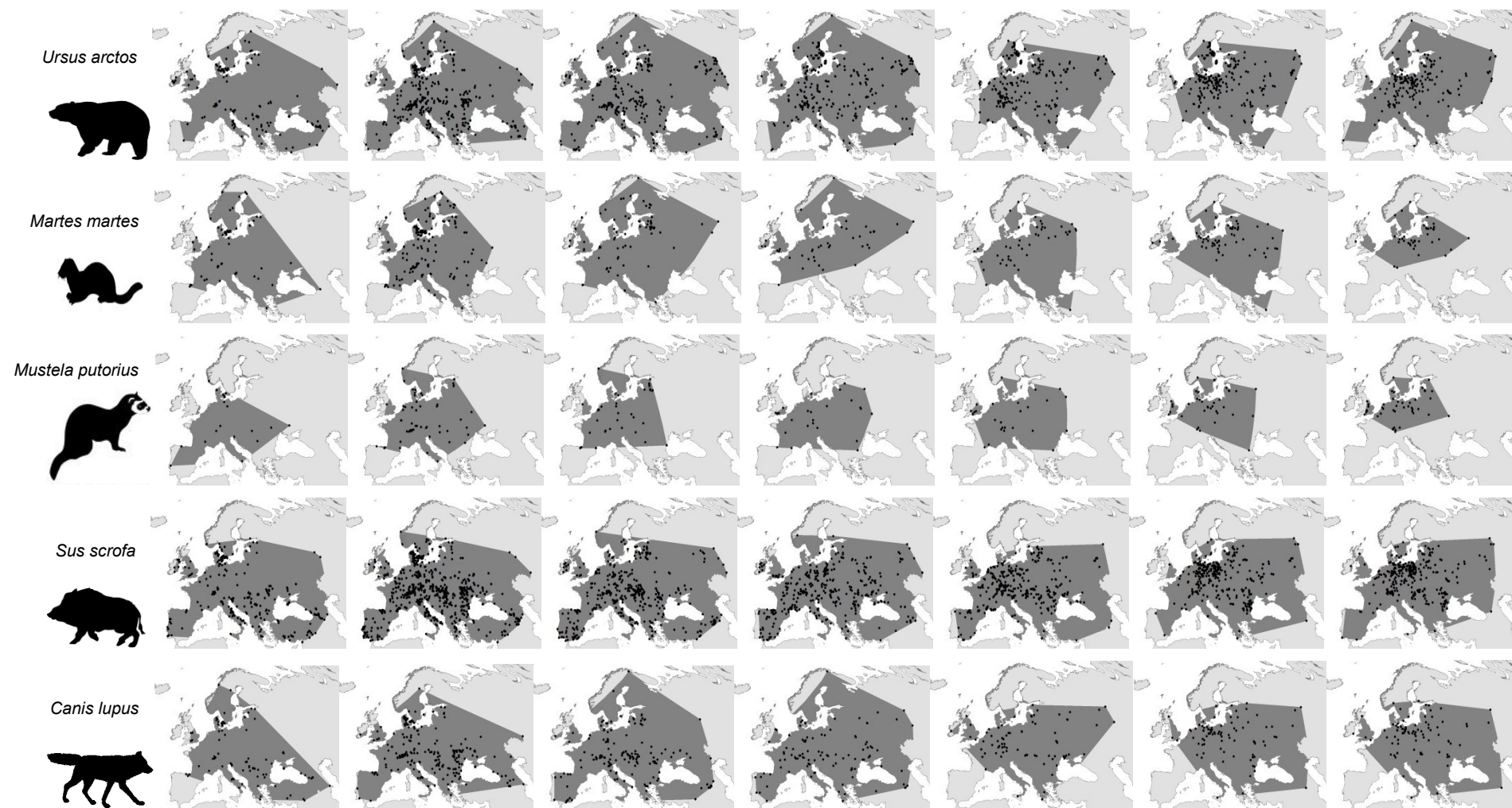
intervals, this was interpreted as representing a genuine, statistically significant deviation from the expected range size for the species. This process was then repeated for each time period for each species.

The number of significant declines was recorded for each species across each time period, with 'decline' noted as a binary variable (0 = no decline, 1 = decline). Chi-squared tests were then used to detect any differences in numbers of declines between time periods and species. A general linear model (GLM) with poisson errors, to account for the response variable being count data, was also used to identify whether the number of declines for each species was associated with specific ecological traits that might affect survival. Selected traits were body mass (g), trophic level (a categorical variable 1-3), diet breadth (a categorical variable from 1-8, with 1 representing a restricted diet consuming only one category of food and 8 representing a highly varied diet consuming up to eight different categories of food), the reproductive variables of interbirth interval and litter size (based on the same rationale as for Chapter 3), home range (km²), and Holocene range (km²). Holocene range data were calculated as the maximum EOO encompassing all known Holocene zooarchaeological records for a species; sources for all other ecological data have been described in Chapter 3. It was suspected that these ecological variables might display collinearity, when two or more variables are linearly related, a common feature of ecological data (Graham 2003). Collinearity tends to increase the standard error of coefficients, thus decreasing the significance of predictor variables even if they are truly influential (Dromann *et al.* 2012) and can also be exacerbated by low sample size of the dependent variable and a high number of independent variables (MacNally 2000). Collinearity was tested for using Variance Inflation Factors (VIF) which measures the variance of the coefficients; in general if VIF is found to be above 10, then collinearity is associated with that variable, although this threshold has been debated (O'Brien 2007). All VIFs were found to be <10 therefore all variables were included in the analysis.

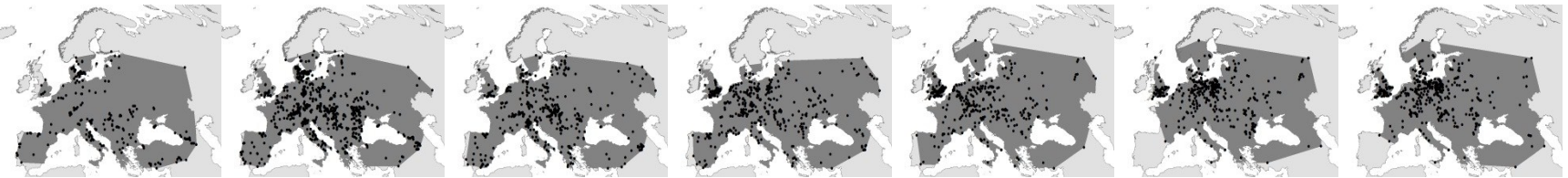
The zooarchaeological record is not commonly used for documenting species occurrences for the Modern period (AD 1500 – present) partly because the focus on archaeological enquiry tends to be for older time periods and also as the written historical record tends to be the predominant source of evidence for this period. If species have become very rare by this time they are also far less likely to appear in the zooarchaeological record, and so it is not necessarily the best source of evidence for the most recent time period. Furthermore, the International Union for the Conservation of Nature (IUCN 2012) provides a relatively detailed assessment of the status of extant species from AD 1500 onwards, so that much of this information is already documented. Initial bootstrapping results further suggested that sample sizes for the Modern period were too low to draw meaningful conclusions on species range dynamics. Therefore these analyses focused on species range changes from the Mesolithic to the Late Medieval (up to AD 1500) only.

5.4 Results

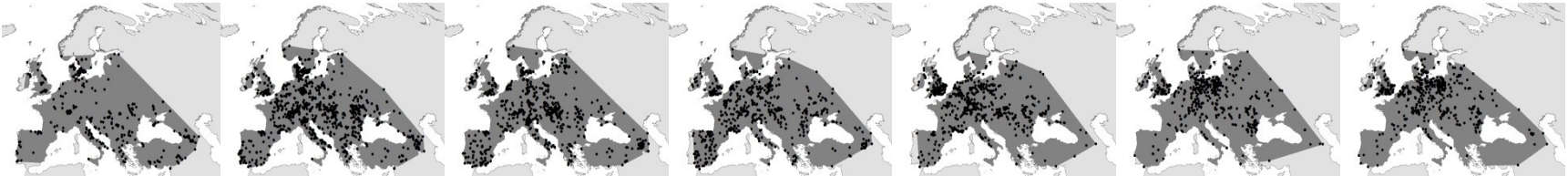




Capreolus capreolus



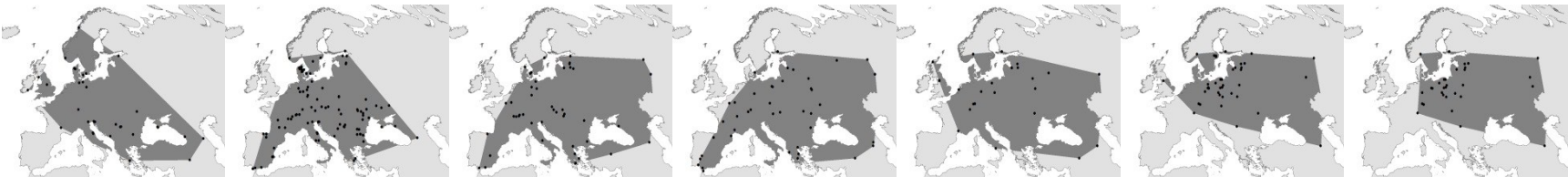
Cervus elaphus



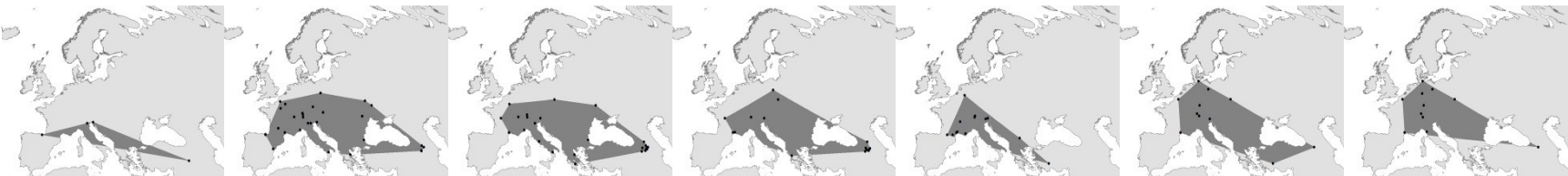
Felis silvestris



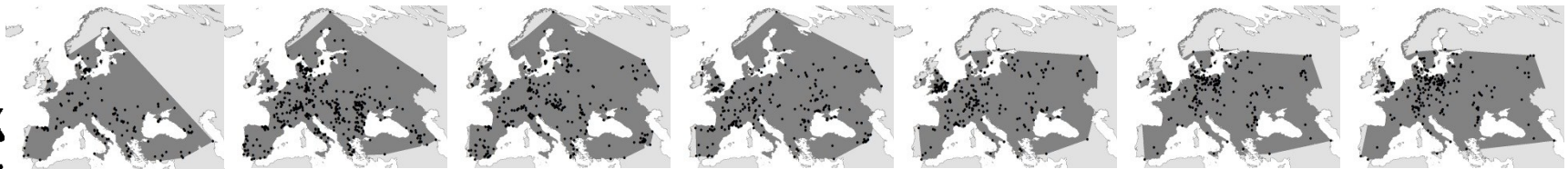
Lynx lynx



Martes foina



Vulpes vulpes



Range restricted species

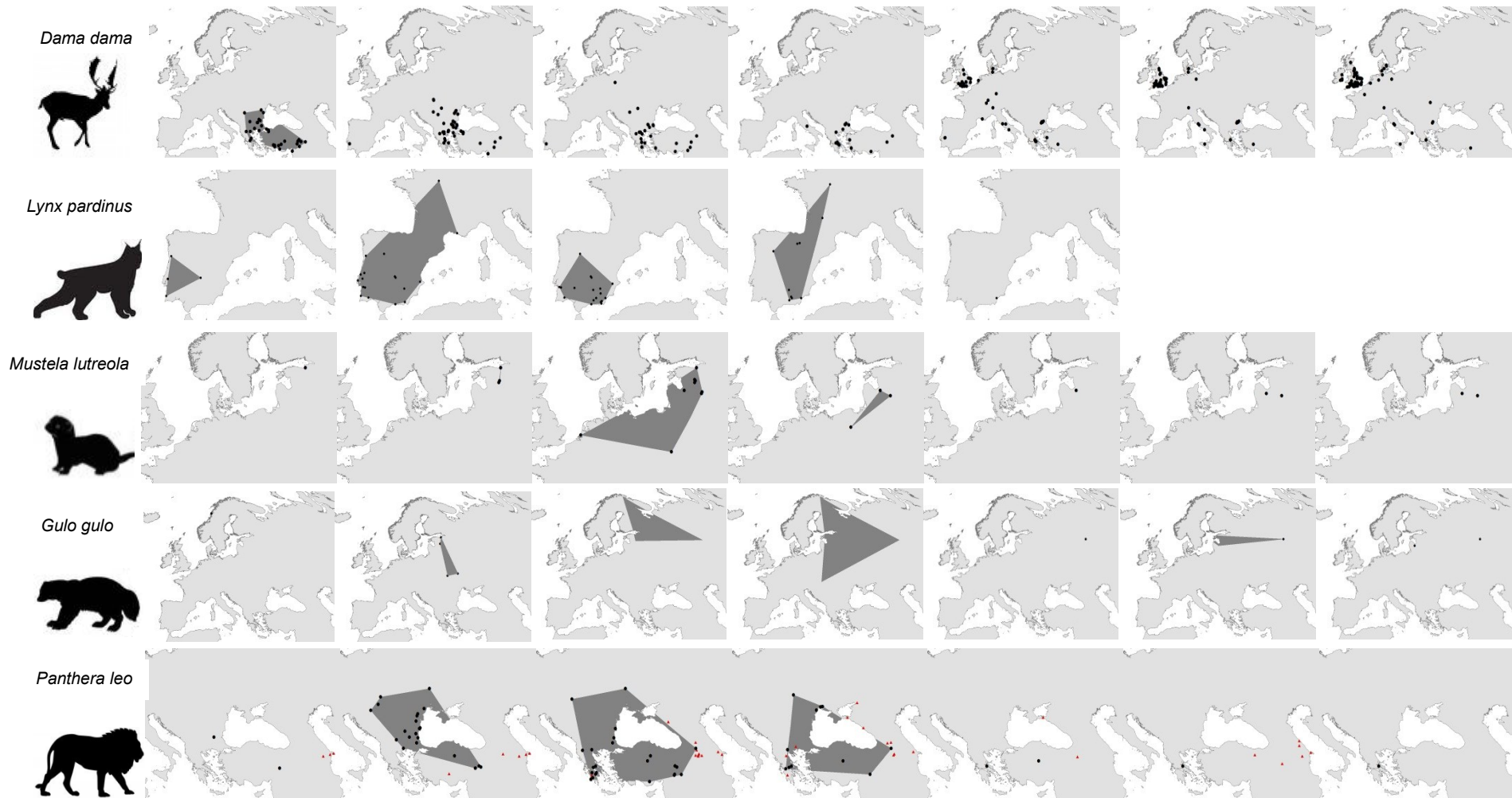




Figure 5.1 Range shifts from the Mesolithic to the Late Medieval, showing extent of occurrence based on zooarchaeological records (black points). The first line of maps shows all zooarchaeological records for each time period. For range-restricted species, red points denote non-zooarchaeological records.

The majority of range shifts occurred in a direction between 0 and 90 degrees, i.e. north to north-east, and secondarily between 270 and 360 degrees, i.e. north-west to north (fig. 5.2). Only two species, elk (*Alces alces*) and red deer (*Cervus elaphus*), shifted in a southerly direction (south-eastwards and south-westwards respectively). However, there was significant variation in the direction of range shifts between time periods ($F = 4.6039$, $df = 5$, $p < 0.001$). Post hoc tests confirmed that the three directional shifts during the latter part of the Holocene (between the Iron Age – Roman Age, Roman Age – Early Medieval and Early Medieval – Late Medieval) were driving the difference, with no significant difference between the earlier three Holocene directional shifts (fig. 5.3).

Between the Mesolithic and Late Medieval, species ranges most frequently shifted between 200-400 kilometres, with only three species, polecat (*Mustela putorius*), beech marten (*Martes foina*) and lynx (*Lynx lynx*), shifting more than 500 km altogether (fig. 5.4). There was no significant variation in the distance shifted between time periods ($F = 0.785$, $df = 5$, $p > 0.1$).

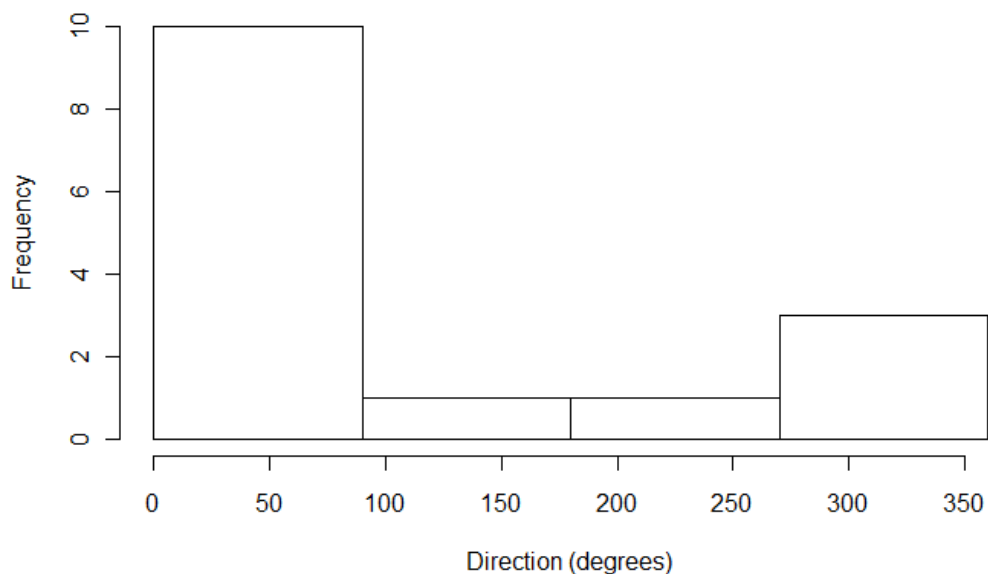


Figure 5.2 Histogram showing overall directional shift of each species from Mesolithic to Late Medieval. Bearing is defined in degrees of a circle, thus 0/360 = north, 90 = east, 180 = south, 270 = west.

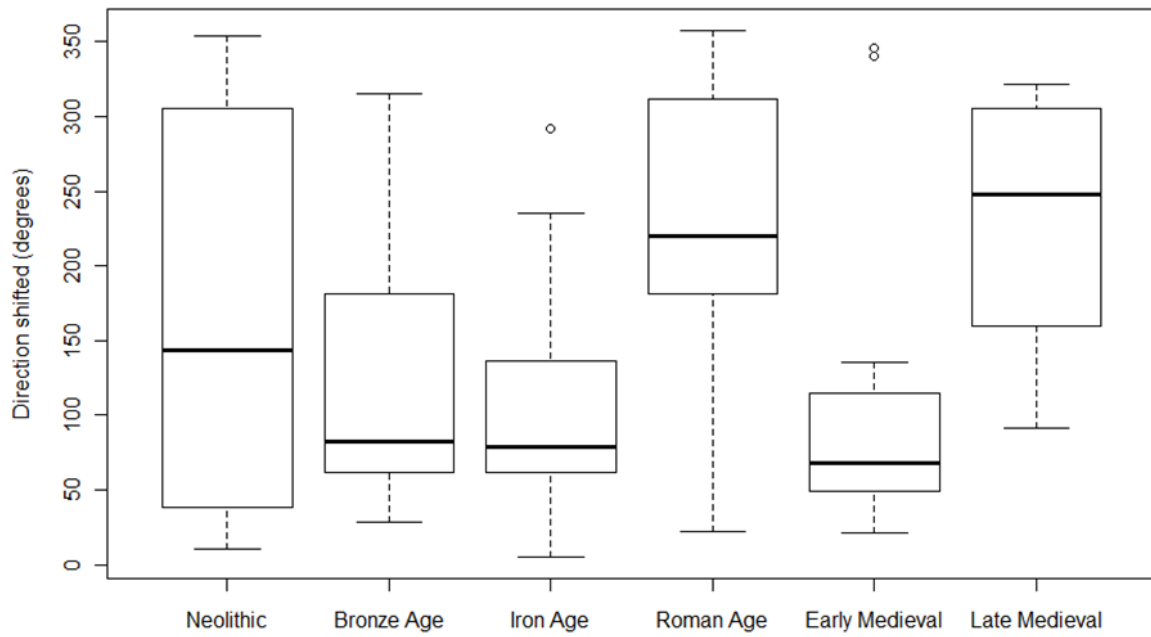


Figure 5.3 Plot of analysis of variance of the overall direction shifted across all species between different time periods. 'Neolithic' denotes the directional shift between the Mesolithic and Neolithic, 'Bronze Age' denotes the shift between the Neolithic and Bronze Age, etc.

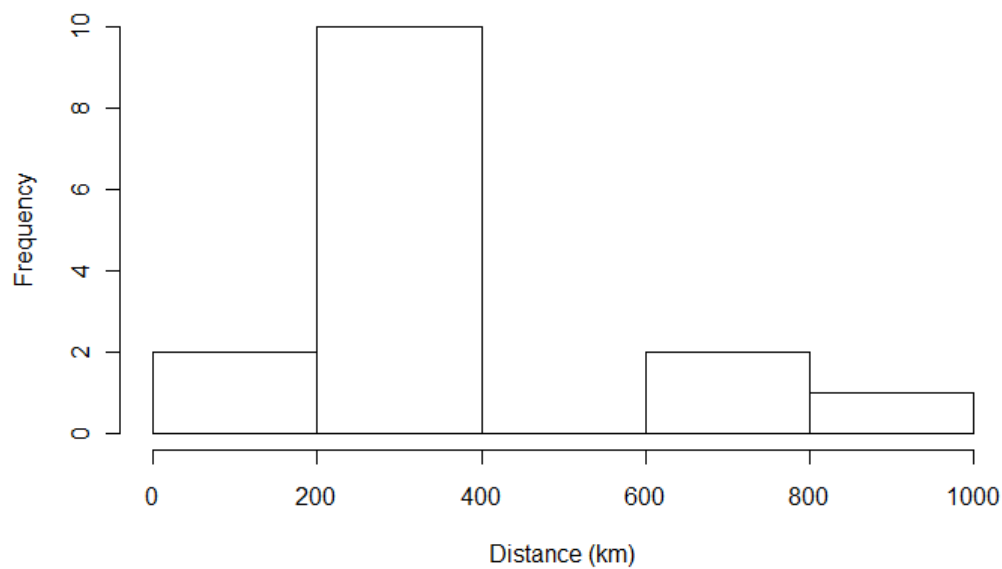


Figure 5.4 Histogram showing overall distance shifted of each species from Mesolithic to Late Medieval in kilometres.

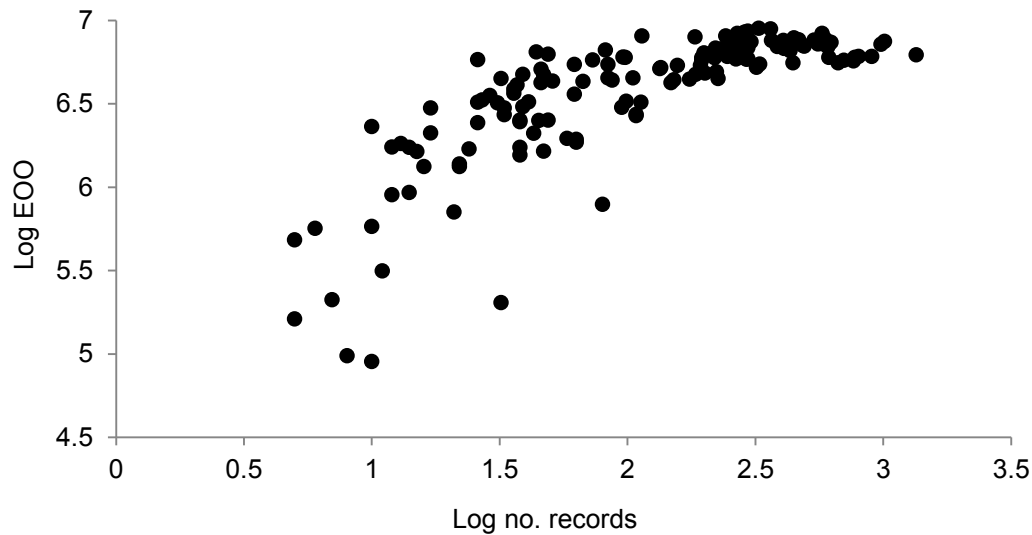
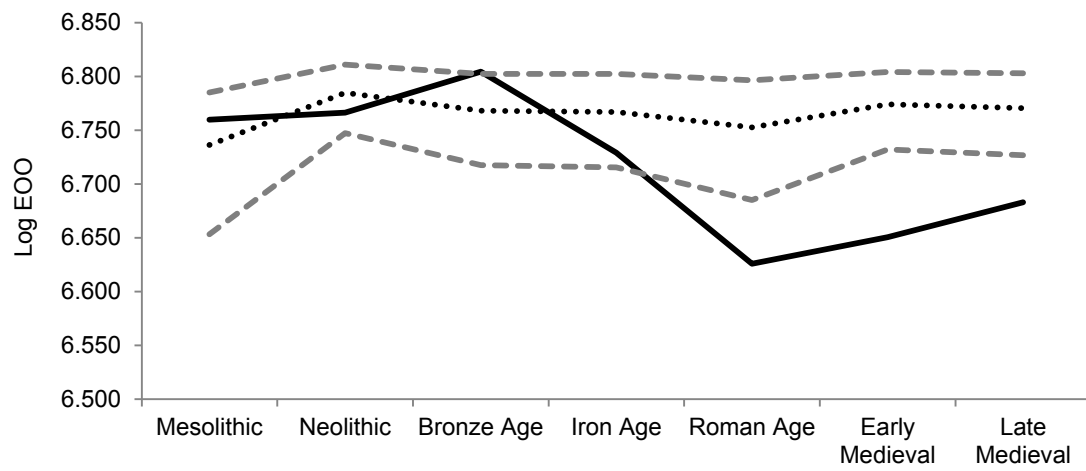


Figure 5.5 The relationship between number of records and extent of occurrence (EOO) for the Holocene zooarchaeological record. Each point represents one species at one time period.

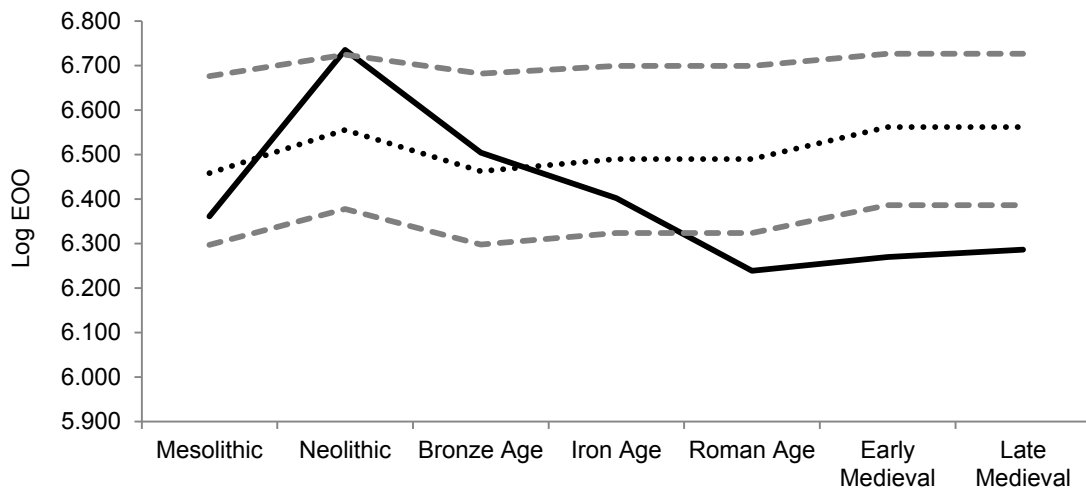
Eight out of fifteen species experienced a significant decline in range by the Late Medieval, starting at different time periods across the Holocene (fig. 5.6; fig. 5.7). Aurochs (*Bos primigenius*) experienced a statistically significant decrease in EOO earlier than all other species, beginning in the Iron Age. Four other species, elk, bison (*Bison bonasus*), beaver (*Castor fiber*) and brown bear (*Ursus arctos*), experienced decreases in EOO from the Roman Age. Three further species, pine marten (*Martes martes*), polecat and wild boar (*Sus scrofa*), declined in EOO from the Late Medieval. By contrast, the remaining seven species, wolf (*Canis lupus*), roe deer (*Capreolus capreolus*), red deer, wildcat (*Felis silvestris*), lynx, beech marten and fox (*Vulpes vulpes*), broadly maintained their range throughout the Holocene (fig. 5.6).



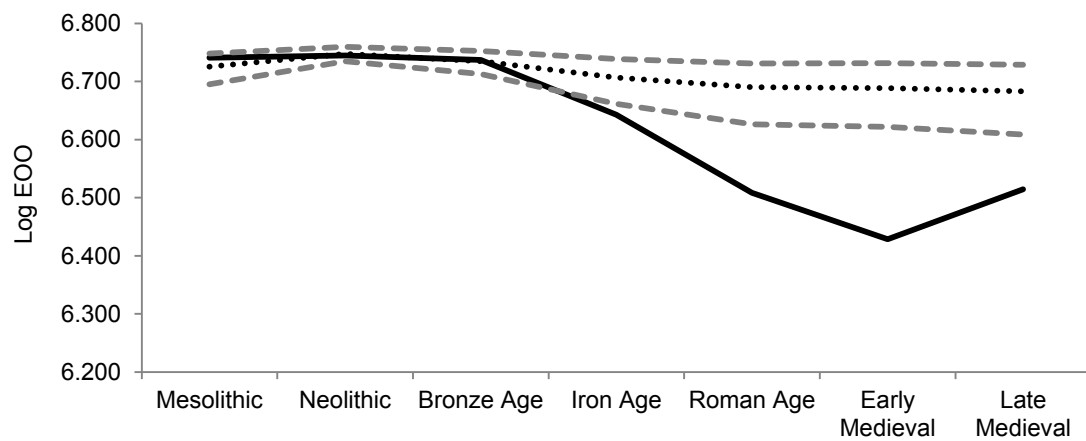
Alces alces



Bison bonasus

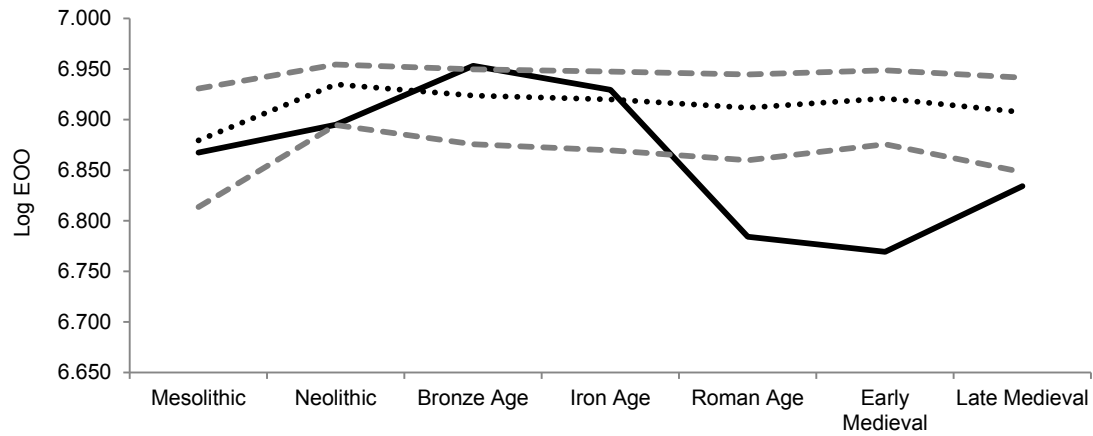


Bos primigenius

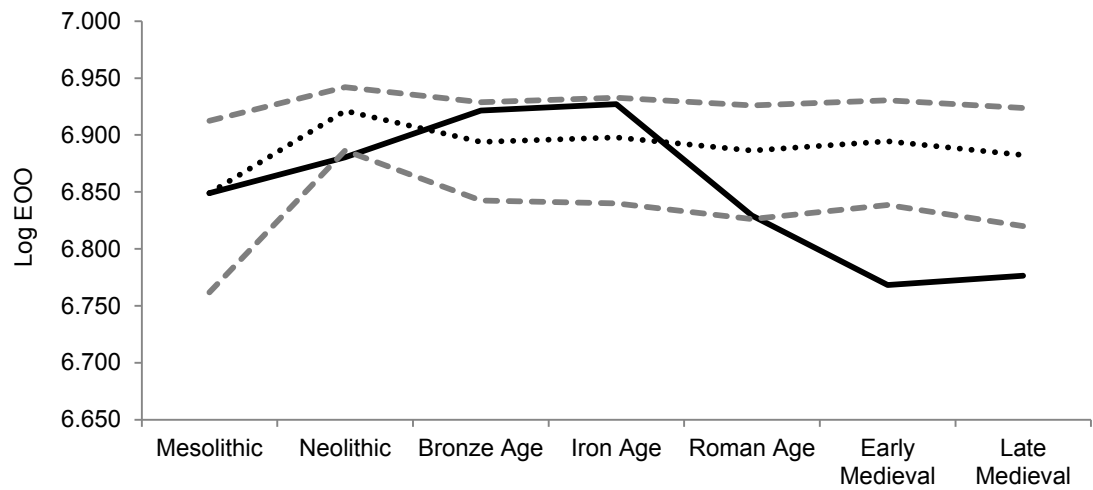




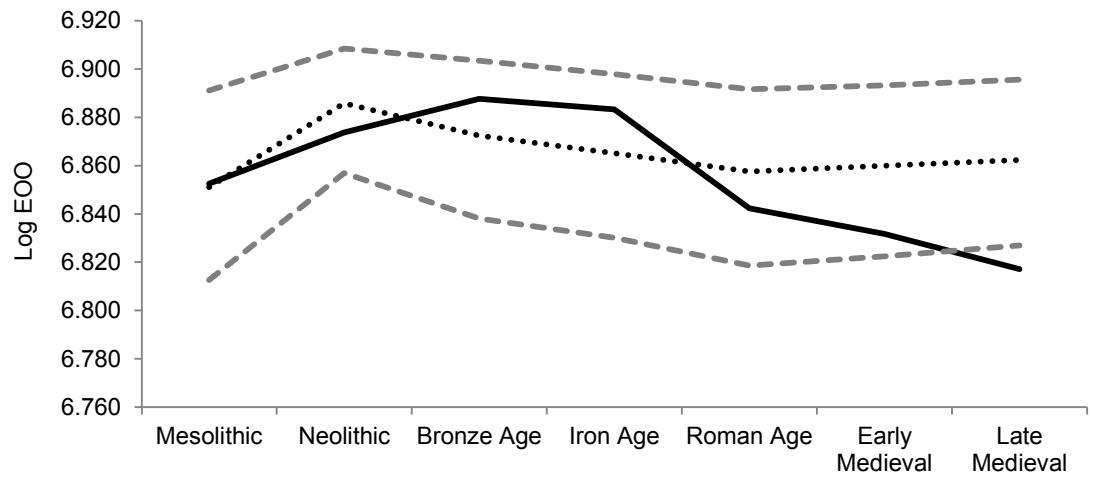
Ursus arctos



Castor fiber

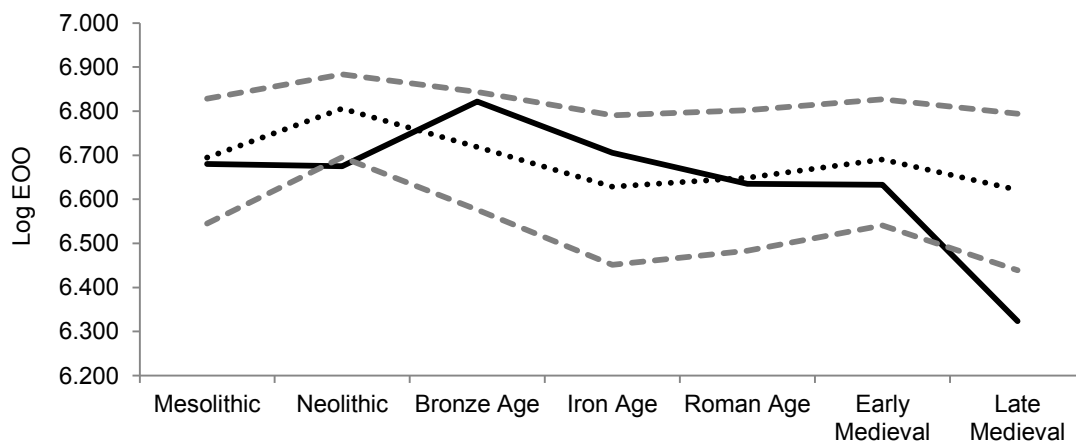


Sus scrofa

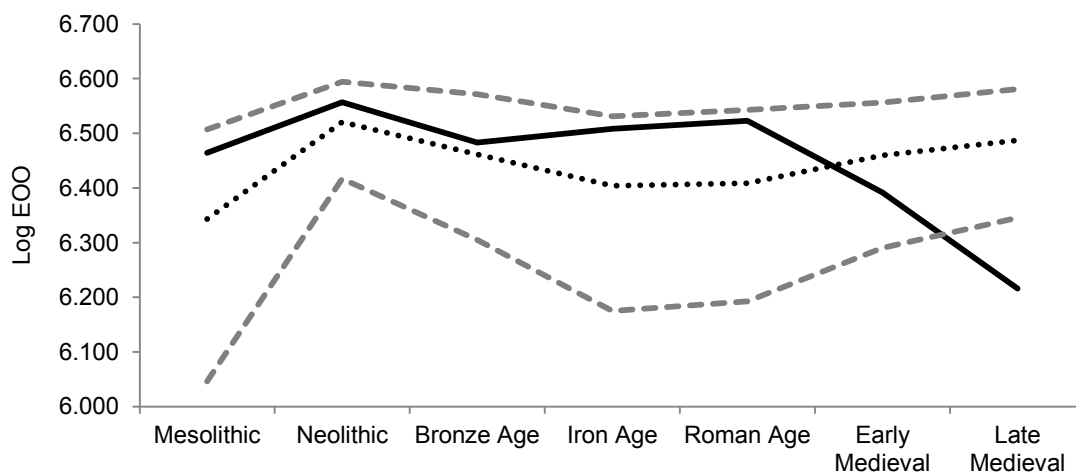




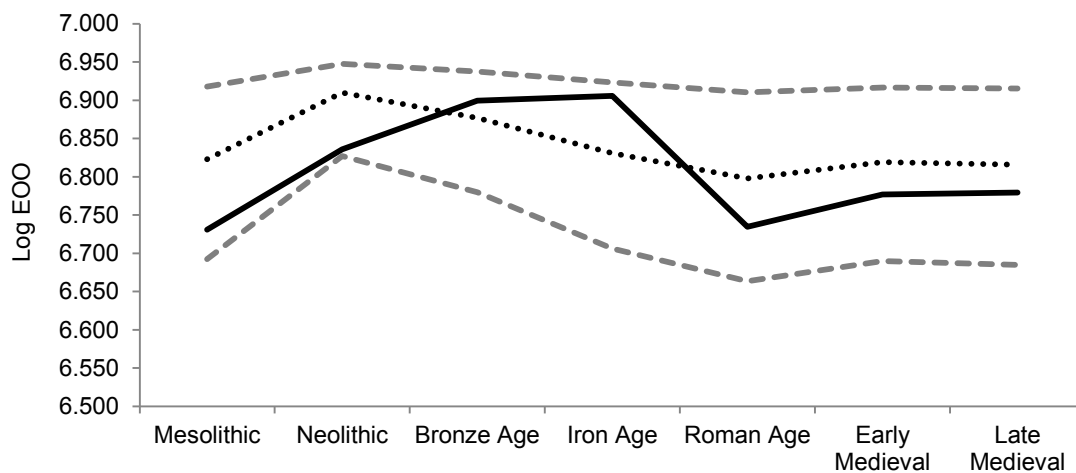
Martes martes



Mustela putorius

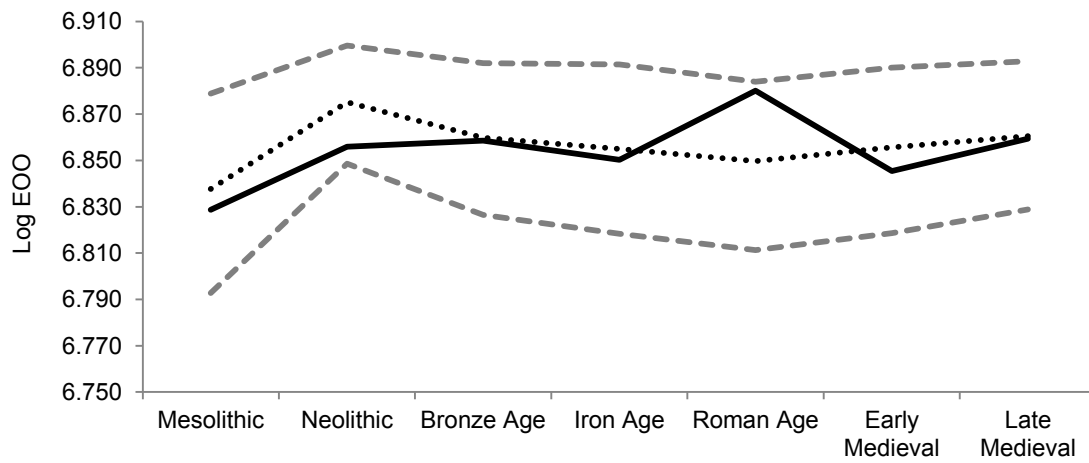


Canis lupus

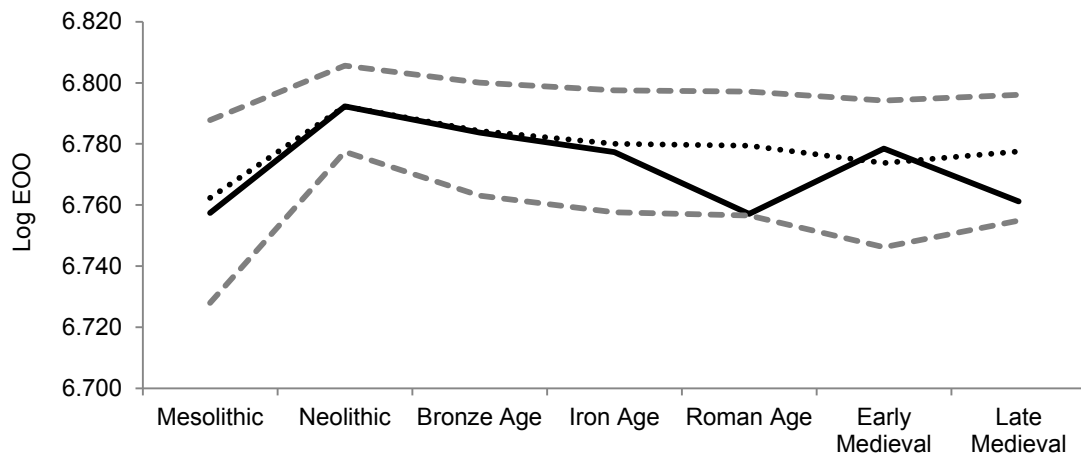




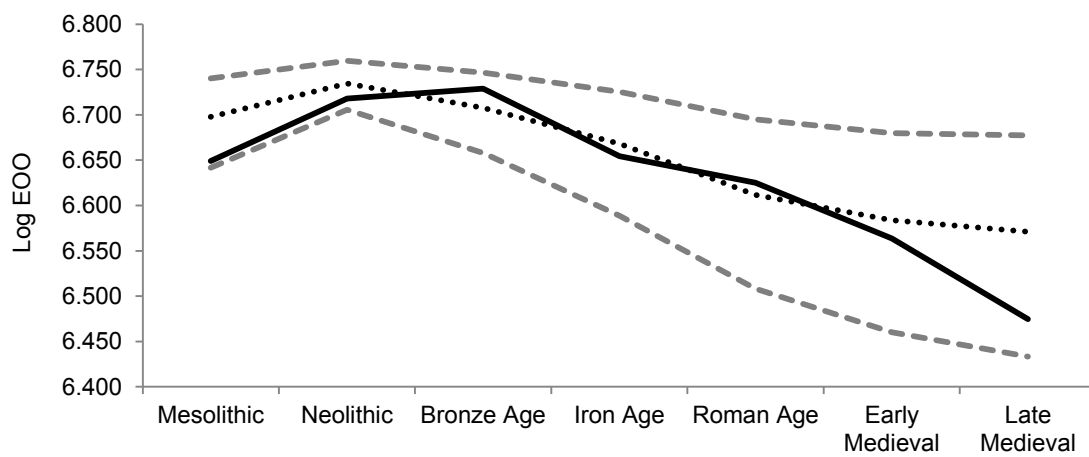
Capreolus capreolus



Cervus elaphus

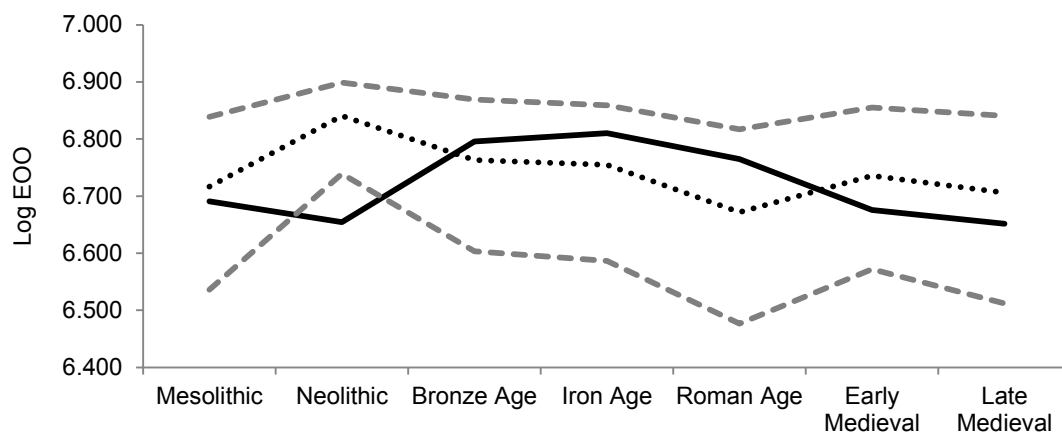


Felis silvestris

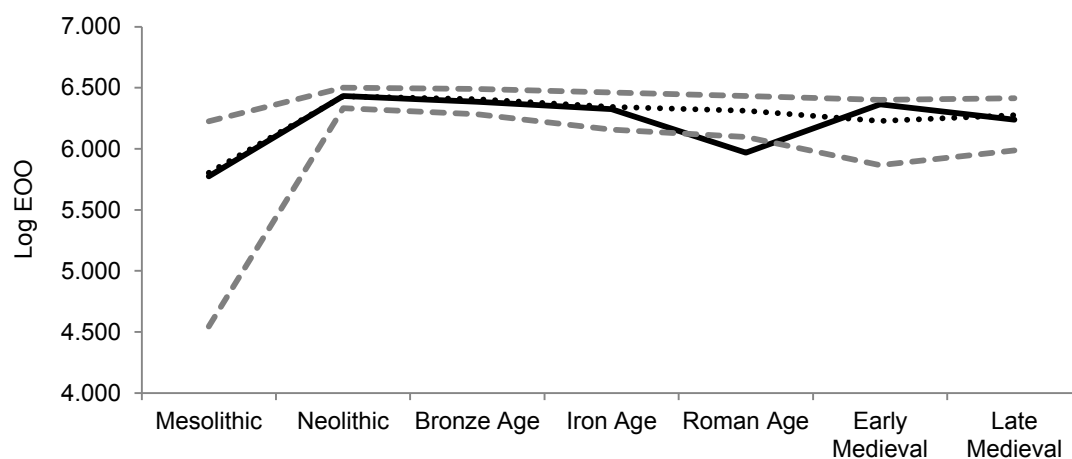




Lynx lynx



Martes foina



Vulpes vulpes

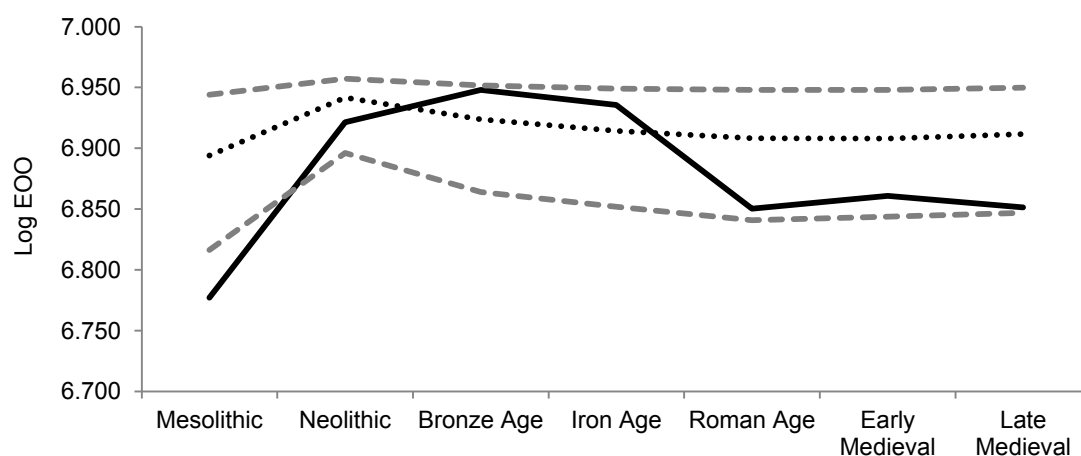


Figure 5.6 Log extent of occurrence (EOO) from the Mesolithic to Late Medieval. Grey dashed lines denote bootstrapped 95% confidence intervals for extent of occurrence (EOO). Black dotted line denotes mean EOO from all bootstrapped samples and solid black line observed EOO.

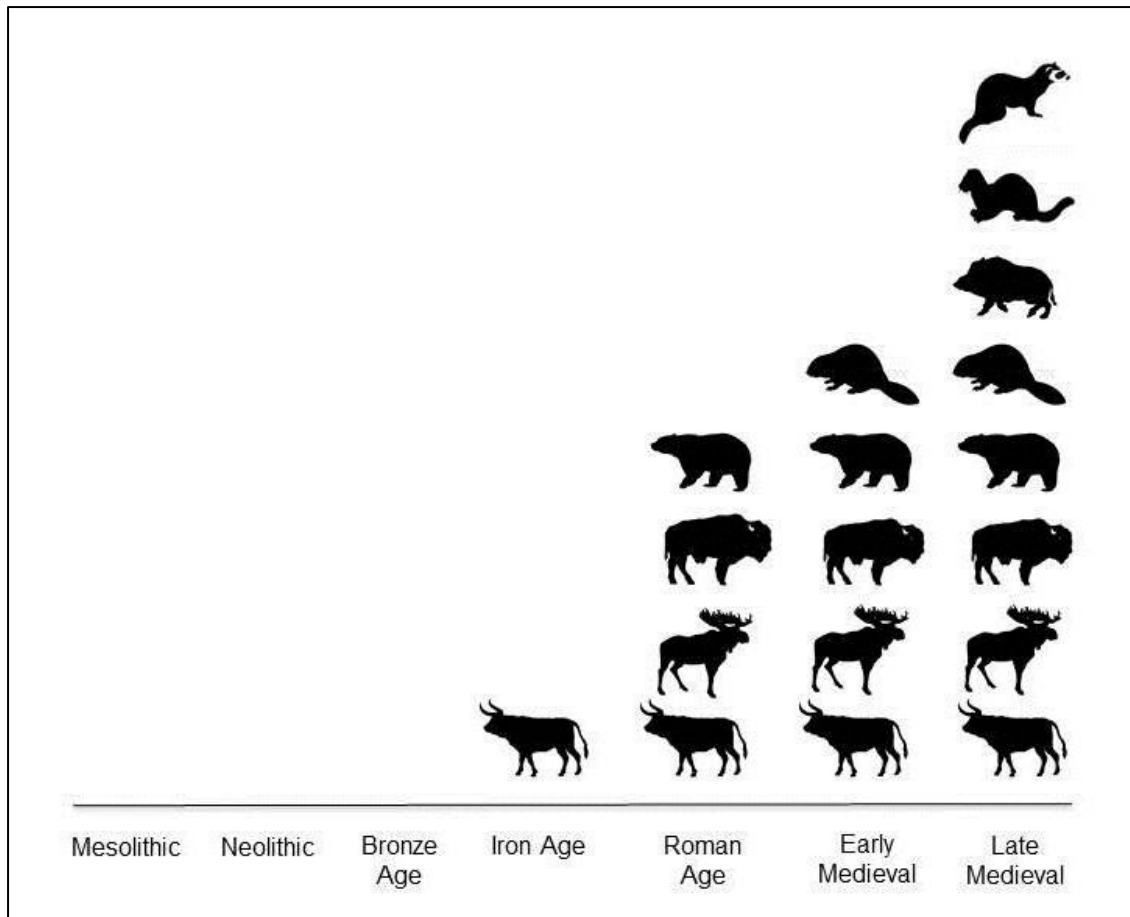


Figure 5.7 Summary of time periods in which specific species experienced a consistent significant decline.

The number of range declines varied significantly between time periods ($\chi^2 = 19.263$, $df = 6$, $p < 0.01$), although not quite between species ($\chi^2 = 21.4899$, $df = 14$, $p = > 0.05$). Under univariate analysis the total number of time periods for each species in which a significant decline occurred was found to correlate significantly positively with body mass and diet breadth and significantly negatively with trophic level (see Appendix 6). However when these were put into a multivariate GLM only level 3 of trophic level was found to be significantly negatively related to mammal declines (-1.946 ± 0.7949 , $p < 0.05$), with lower numbers of declines associated with higher trophic level.

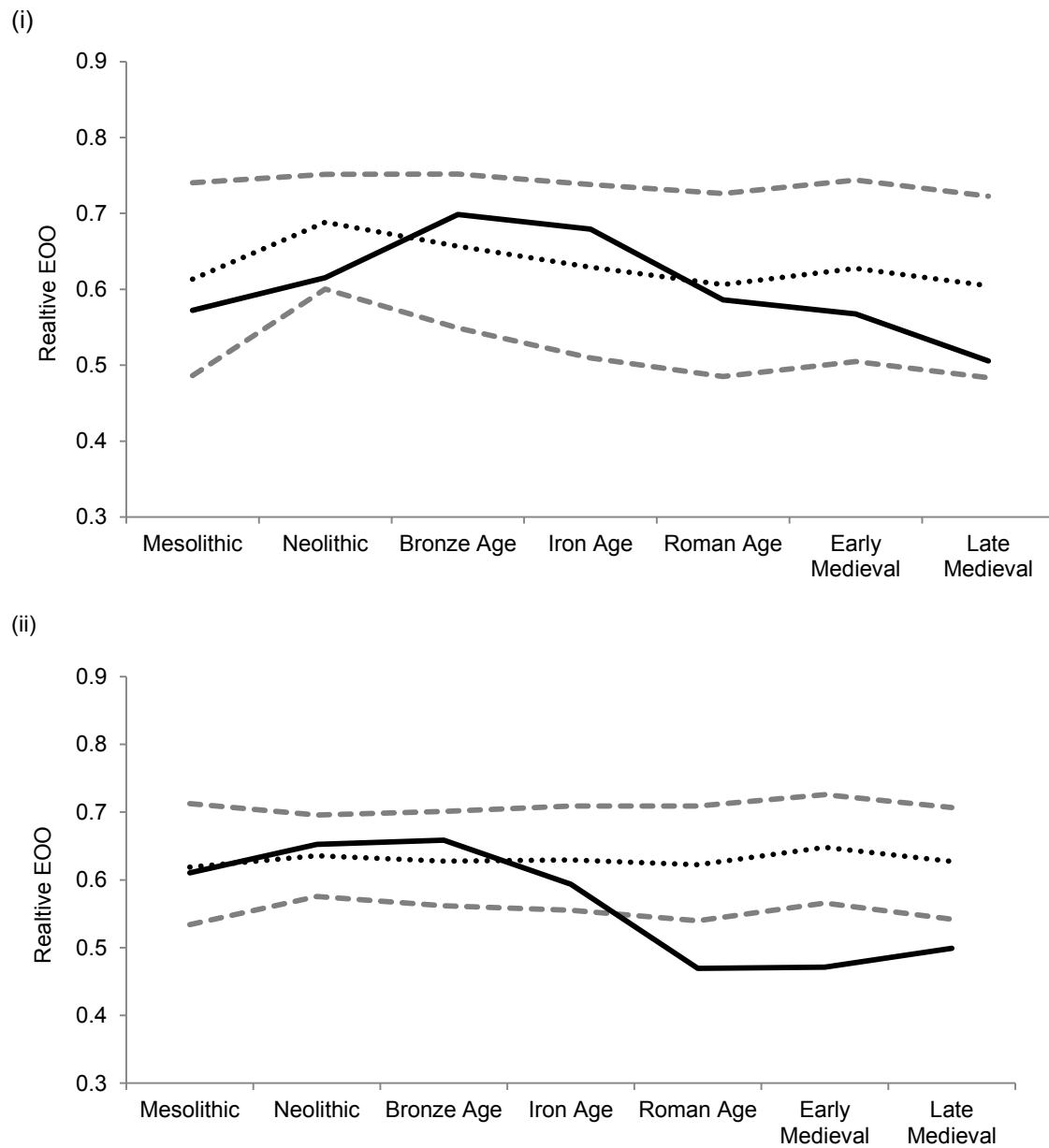
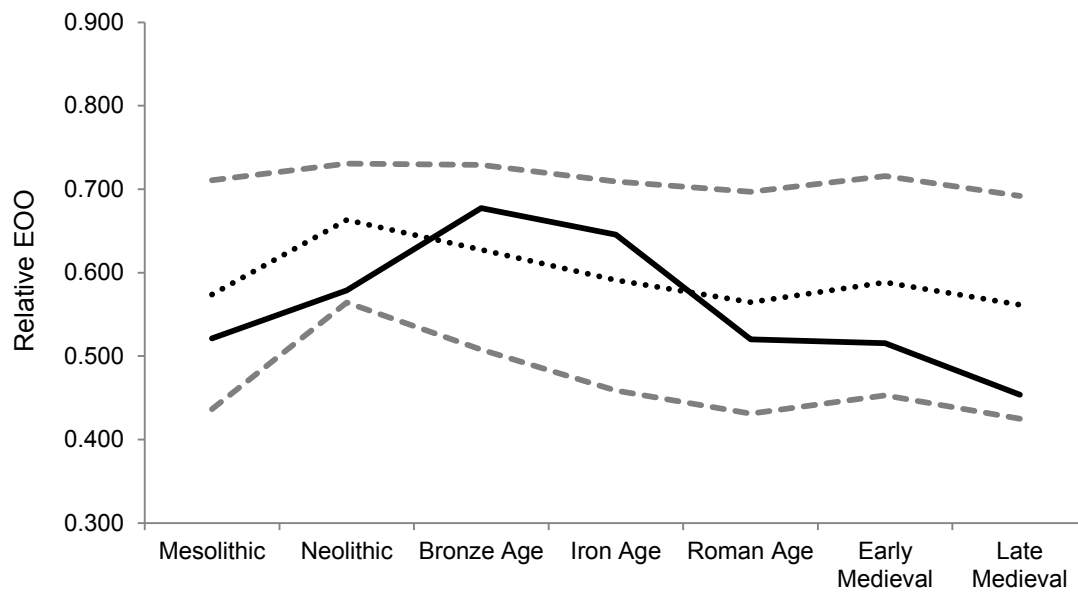


Figure 5.8 Observed average extent of occurrence (EOO), and expected average EOO based on bootstrap models, across all time periods for i) species <100 kg, and ii) species >100 kg. All calculations are on a relative scale.

(i)



(ii)

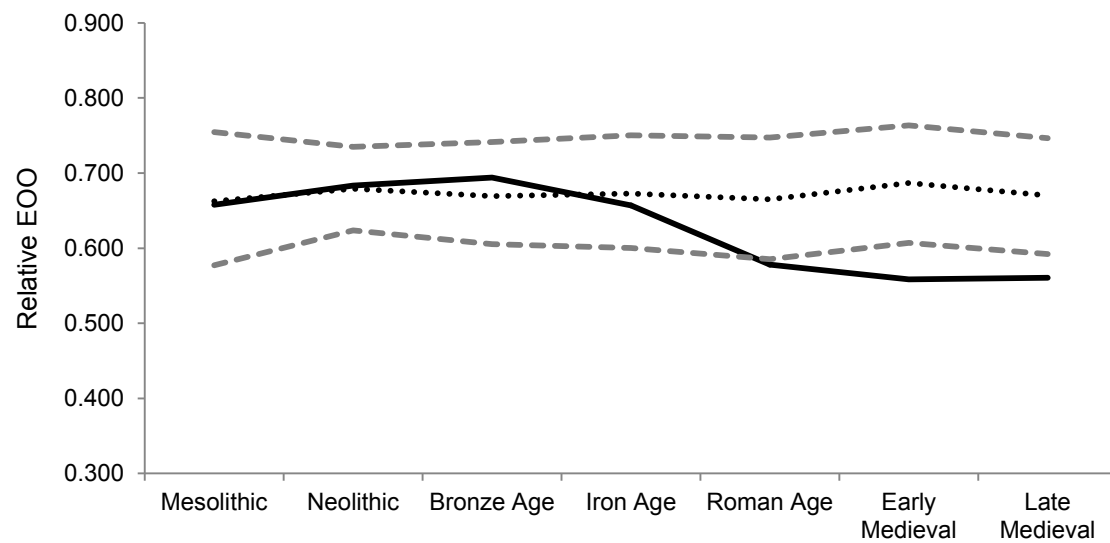
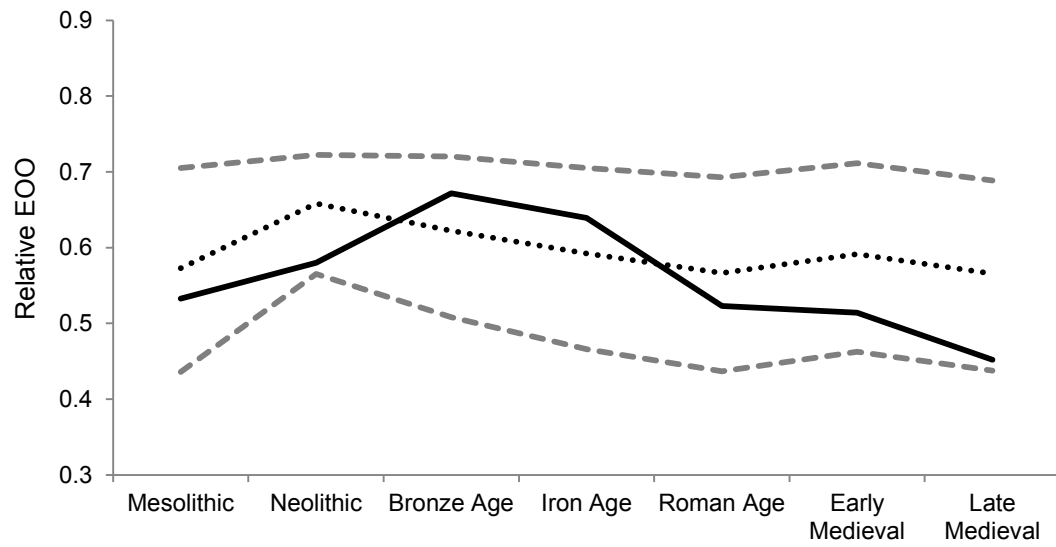


Figure 5.9 Observed average extent of occurrence (EOO), and expected average EOO based on bootstrap models, across all time periods for i) carnivores and ii) herbivores. All calculations are on a relative scale.

(i)



(ii)

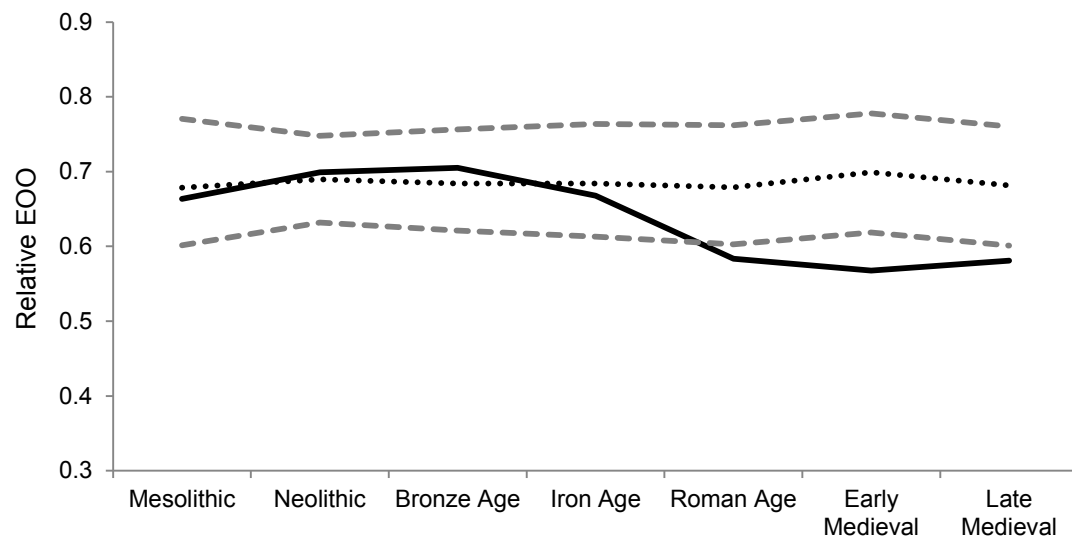


Figure 5.10 Observed average extent of occurrence (EOO), and expected average EOO based on bootstrap models, across all time periods for i) diet breadth, level 1 and ii) diet breadth, level 2+. All calculations are on a relative scale.

5.5 Discussion

5.5.1 Spatial patterns of range shifts

The Holocene zooarchaeological record was a substantial data source, allowing for the relatively detailed reconstruction of mammal distributions across a range of species and through time (fig. 5.1). For species with a restricted distribution, there was generally a paucity of raw data for consecutive time periods, limiting the ability to infer continuous spatial patterns of declines. Nevertheless, for species such as lion (*Panthera leo*), even though zooarchaeological data was reduced to only two or three records in latter periods, general congruence between zooarchaeological and historical records allowed for some interpretation of range dynamics. In this case for example, the data indicated a 'pulse' of range expansion from Turkey into south-eastern Europe between the Mesolithic and Bronze Age followed by a contraction back into its original range from the Iron Age onwards (fig. 5.1). By contrast, for other species such as Iberian lynx (*Lynx pardinus*), extremely marked fluctuations in range were probably the result of patchiness and low abundance of faunal records rather than actual range dynamics.

Overall centroid shifts for widespread species indicated that in general, large mammal ranges shifted north-eastwards during the Holocene (fig. 5.2). The fact that significant variations in the direction of range shifts began between the Iron Age and Roman Age (fig. 5.3), which coincided with the same time period in which the first significant range declines occurred (fig. 5.7), also suggested that centroid shifts were probably related to range contractions. These patterns are supported by the current biogeographic pattern of a decrease in species richness westwards across Europe (Baquero and Telleria 2001). Rodriguez *et al.* (2006) also found that current mammal body size distribution decreased westwards, with the smallest mean body sizes found in southern Britain, France, Germany and the Low Countries, which the authors associated with higher human population densities and therefore higher levels of extirpation of large-bodied species in these regions. Indeed, human populations in western Europe are thought to have grown more rapidly than those in eastern Europe throughout prehistory (McEvedy and Jones 1978).

In terms of biogeography, southern Europe also consists of three major peninsulas (Iberian, Italian and Balkan), and whilst these have provided refugia during previous periods of climatic change (Sommer and Nadachowski 2006; Weiss and Ferrand 2007) they may have served to fragment and isolate mammalian populations already under pressure from high human populations, pushing ranges northwards. This could have been particularly exacerbated on the Iberian and Italian peninsulas whose continental edges are both bordered by large mountain ranges, thus potentially providing barriers to dispersal for mammal species that could not adapt to areas of higher elevation, such as principally lowland-dwelling large herbivores (Hall 2008).

The overall shift of ranges towards the north-east broadly supports the contagion model of species range contraction (Caughley 1994; Lomolino and Channell 1995) in which range collapse occurs

across the range from one side to the other rather than from the range periphery towards the centre. This makes sense within the context of long-term anthropogenic extinction drivers, as the major human innovations that fuelled population growth during the Holocene, such as agriculture and the emergence of cities, generally developed in one area and subsequently spread in 'waves' across Europe (Ammerman and Cavalli-Sforza 1971; Antrop 2004; Pinhasi *et al.* 2005). The similarity in overall distances shifted between time periods indicated that such range shifts occurred at a relatively steady rate, with no sudden overall collapse across species. However, the variation in direction of the shifts between time periods (fig. 5.3) suggests that spatially, range collapse was not a linear, continuous process as suggested by Channell and Lomolino's (2000a, b) model based on a simple historic-present range. Rather, dynamic shifts back and forth probably occurred within an overall directional shift, albeit on a small scale.

5.5.2 Data variability

Unfortunately an analysis of range centroids was not as informative about the spatial dynamics of range contraction as for example, a more specific focus on movements of range edges would have been. However, the location of range edges, which were based on the outermost records, was subject to some random fluctuation from one time period to another (fig. 5.1). This analysis was therefore restricted to an assessment of directional shifts based on the location of centroids, as it was felt that this measurement was less susceptible to variability in sampling bias.

Minimum convex polygons are somewhat coarse and susceptible to overestimating range but they are recognised as capturing the specific measure of the geographical spread of a species and therefore the exclusion of discontinuous areas of distribution to try and 'improve' the method has been strongly discouraged (Gaston and Fuller 2009). However, given the irregular shape of Europe this meant that some species were represented in areas for which there was little or no historical or zooarchaeological evidence. For example roe deer, red deer and wild boar were depicted as inhabiting small areas of Finland despite an absence of postglacial records (Ukkonen 1993) and beaver was also depicted as occupying large portions of southern Italy when it is only known from the far north (fig. 5.1).

There were also some probable discontinuities in the zooarchaeological record that caused artificially fluctuating range dynamics from one time period to another. For example, contrary to the pattern for all other species the Eurasian lynx appeared to decline in the Neolithic, yet scrutiny of the data showed that the source of this pattern was a gap in the zooarchaeological record for lynx in the British Isles from the Neolithic to the Bronze Age. The species reappeared again in the Roman Age and the last record was then known from the Early Medieval, dated to 1550 ± 24 ^{14}C yr BP (Hetherington *et al.* 2006). Being an island it was unlikely that this represented a genuine extinction and re-colonisation event but rather reflected its rarity in the zooarchaeological record as a whole, since only five reliable postglacial records of lynx are known from the British Isles. However, almost all of the species for which such fluctuations occurred were specialist or ecologically rare/range restricted carnivores which

were also consistently rarer in zooarchaeological assemblages across time. This has potential implications for the suitability of using bone assemblages to track past distributions of certain species or species groupings. Whilst not within the remit of this study to fully investigate, this could be a topic that merits future attention.

However, the potential bias that was most concerning was that the number of zooarchaeological records for each species at each time period was positively correlated with the subsequent area of the EOO calculated (fig 5.5). Due to the fact that the quantity of zooarchaeological records varied temporally and across species (fig. 5.1), changes in absolute range calculated on the raw data alone could therefore simply be reflecting variability in the data. Unfortunately, this does suggest that the zooarchaeological record, as an incomplete and biased data source may not be ideal for the precise spatial reconstruction of past species ranges, particularly using standardised methods from ecology.

5.5.3 Temporal patterns of mammalian range shifts

However, whilst the zooarchaeological record may have had limitations for the analysis of absolute spatial dynamics of range decline, the use of bootstrapping proved a powerful tool that allowed for the analysis of relative temporal patterns of range decline. This was particularly important as the observed data alone indicated that almost all species declined in range towards the Late Medieval, yet under bootstrapping constraints, only half of all mammal species showed a statistically significant decline (fig. 5.6). It would therefore have been easy to over-interpret past declines and assess range contractions as occurring at a much earlier stage. Interestingly, this also suggests that zooarchaeological data has the potential to yield substantial underestimates of species ranges when reconstructed using EOO, contrary to concerns of overestimation of species ranges using EOO when based on ecological data (Gaston and Fuller 2009).

Geographical range is a feature of a species' ecology that is inherently dynamic in response to changing environmental conditions but is often treated as static (Channell and Lomolino 2000b) despite our understanding of past climatic and anthropogenically-driven changes to the European landscape (Roberts 1998). Therefore significant declines in mammal ranges (fig 5.6; fig. 5.7) can be interpreted within the relatively robust framework of known postglacial environmental change that has taken place over the past several thousand years.

Large mammal ranges at the Pleistocene-Holocene boundary were in flux due to the rapid climatically-driven environmental change that took place at the end of the last Ice Age glaciation, and cold-adapted faunas previously spread across the steppe tundra of northern and central Europe were shifting their distributions in response to retreating ice sheets and woodland expansion (Stuart *et al.* 2004). At the same time temperate-adapted species were moving out of their glacial refugia, both in southern Europe (Sommer and Nadachowski 2006) and northern Europe (Stewart and Lister 2001). The factors that limit ecological ranges are still debated (Fortin *et al.* 2005; Gaston 2009) and the relative contribution of climate *per se* and climate-induced forest expansion on influencing postglacial

species ranges is unfortunately not clear. Postglacial climate change was extremely rapid in some areas of Europe, occurring as quickly as within 50 years in Britain for example (Yalden 1999), but may have taken longer to stabilise in other areas of Europe (Davis *et al.* 2003). Likewise, palaeoecological evidence indicates that postglacial migrational lags in plant species ranges occurred (Normand *et al.* 2011) and that forests were still expanding at the beginning of the Holocene (Huntley and Birks 1983; Roberts 1998; Kleinen *et al.* 2011). Observed data on EOO did suggest that many large mammal species increased in range from the Mesolithic to the Bronze Age (fig. 5.6), but these occurred within bootstrapped limits so could not be considered significant.

However the same climatic change also caused rapid rises in sea levels across the globe which quickly cut off the British Isles from the mainland around 8600 ¹⁴C yr BP (Anderson *et al.* 2013), with the result of halting the advance of some species ranges during their expansion. For example, white-toothed shrews *Crocidura russula* and *C. leucodon*, failed to reach the UK despite occurring right up to northern France, although there is some debate as to whether the English Channel coincided with the limits of their climatic niche (Yalden 1999). Whilst there may have been a brief land-bridge between the British Isles and Ireland following de-glaciation (Devoy 1985; Lambeck 1995) this was probably too short-lived to have allowed full-scale colonisation of postglacial faunas, and several large mammal species such as beaver, elk, aurochs and roe deer failed to colonise Ireland before sea levels rose (Yalden 1999). However, where species did reach these areas they rapidly became isolated following sea level rises and most likely suffered from the cumulative risks associated with island populations (Diamond 1984; Frankham 1998). Some of the earliest extirpations across Europe e.g. of lynx, bear, elk and aurochs, occurred in Ireland and Britain (fig. 5.1). Even where areas of land were not entirely geographically cut off, similar patterns were caused by the effective isolation of populations. In southern Sweden for example, populations of bison, aurochs and wildcat arrived whilst the land bridge across the Baltic Sea was still intact at the Pleistocene-Holocene boundary but quickly became isolated by around 10000 - 9000 BP once it flooded (Rankama and Ukkonen 2001). As these species were at their latitudinal limit and thus unable to disperse northwards, populations became confined to this small area and their disappearance from the zooarchaeological record in this region was also documented in the Early-Mid Holocene (fig. 5.1). Denmark, whilst not entirely cut off from mainland populations, was reduced to a large isthmus and several islands following sea level rises and again, relatively early-mid Holocene extirpations of elk, bison, aurochs, beaver, wildcat, lynx and bear occurred (fig. 5.1). Thus the range extents of species distributions were already heavily shaped by their environment in the first half of the Holocene.

The ameliorated and more temperate climate after the Late Glacial Maximum also facilitated populations of *Homo sapiens* to expand and it is from the early Holocene onwards that exponential growth of human populations based on advances in food production and technology took place (Diamond and Ordunio 1997). Recent models of prehistoric deforestation suggested that forest loss was already relatively widespread across Europe from around 1000 BC (Kaplan *et al.* 2009). This timing coincided with the beginning of observed significant mammalian range reductions around the

Iron Age and which were particularly marked for large herbivores such as aurochs, bison and elk, as well as the omnivorous brown bear (Cicnjak *et al.* 1987; Clevenger *et al.* 1992, although see also Persson *et al.* 2001; Bojarska and Selva 2011), (fig. 5.7). Regional palaeoecological studies have also confirmed widespread deforestation prior to the Roman Age, and provided further details of regional patterns of human-driven habitat degradation and destruction. For example, in England forest loss was identified earlier than Roman arrival (Dumayne 1993; Manning *et al.* 1997), where both elk and aurochs regionally disappeared from the zooarchaeological record by the Iron Age (fig. 5.1). In Northwest Portugal pollen analysis has also detected vegetation shifts consistent with deforestation from the Bronze Age onwards (Figueiral 1995), and the zooarchaeological record indicates that several large mammal species disappeared from this region by the Iron Age (fig. 5.1). The historical record additionally confirms the manner in which humans were altering natural landscapes, with classical writers such as Homer documenting European land clearance from as early as 900 BC (Williams 2000).

Unfortunately the extent to which Holocene large mammals were dependent on forests *per se* as an ecological/habitat niche has not been well studied. This is partly due to the ongoing debate regarding the degree of 'openness' and structure of early Holocene forests and whether large herbivores maintained a patchwork mosaic of forest and open areas or relied on a closed forest environment. Vera (2000) first proposed the theory of postglacial herbivore-driven open landscapes and, whilst palaeoecological evidence has supported the presence of mixed open-woodland, the drivers of these habitats have more recently been attributed to human activity (Bradshaw 2004; Mitchell 2004; Birks 2005) as well as autogenic disturbance (Whitehouse *et al.* 2004) rather than large mammal faunas. Furthermore the synergistic effects of deforestation/habitat loss and associated increases in human hunting facilitated by more open landscapes, makes it effectively impossible to tease apart the relative significance of forest loss *per se* as a driver of Holocene mammalian extinctions (Marchant *et al.* 2009). However humans were clearly fragmenting the landscape at a continent-wide level, and agriculture and human settlement were likely to have presented substantial barriers to dispersal and greatly reduced the available land area for large mammals to survive, even if forest presence itself was not the primary influence on large mammal ranges.

The rate of decline of many mammal ranges appeared to decelerate somewhat in the Early-Late Medieval (fig. 5.6), although not significantly so. It is possible that this was an effect of the Black Death, which occurred in Europe in AD 1347-1351 and drastically reduced Europe's human population by somewhere between twenty-five and fifty percent (Gottfried 2010). Pollen studies have confirmed that in many areas of Europe this led to agricultural regression and forest regrowth, and even associated climatic impacts (van Hoof *et al.* 2006; Yeloff and van Geel 2007). Whilst this is not likely to have given already reduced large mammal populations time to fully regenerate, especially given any time lag effects that might be expected in association with such a recovery, it might have been sufficient to lead to a deceleration in range declines and in some areas small opportunities for range expansion.

This study highlighted that prehistoric faunal records are essential for understanding temporal extinction dynamics in regions with a long history of human presence such as Europe, where large mammal declines began much earlier than AD 1500, which is the current benchmark for assessing extinction (Temple and Terry 2007). It also provides a note of caution against underestimating the effects of even relatively low levels of human activity on mammal persistence. A long-term perspective across the large mammal guild also reveals that individual species' declines have not been temporally congruous throughout the Holocene (fig. 5.7), mirroring Late Quaternary extinction patterns across the Pleistocene-Holocene boundary (Stuart and Lister 2007; Lorenzen *et al.* 2011). This is particularly interesting given that the principal driver was probably different for each extinction episode, with climate change strongly promoted as being the primary (though not only) extinction driver for Late Pleistocene megafaunal extinctions in Europe (Stuart and Lister 2007) and human activity the primary driver of Holocene mammalian declines (Turvey 2009b). The species-specific nature of the extinction of Europe's large mammal fauna is most plausibly linked to the theory that extinction risk in large mammals is driven by the interaction between both extrinsic and intrinsic factors (Cardillo *et al.* 2005), meaning that extinction dynamics are likely to vary across species with different life histories even if they are facing the same external threat processes.

5.5.4 Life history traits associated with range shifts

Geographic range size is an ecological trait associated with characteristics such as body mass (Brown and Maurer 1989), dispersal ability (Brown *et al.* 1996) and extinction risk (Purvis *et al.* 2000b), and therefore changes in species ranges should also be interpreted within the context of intrinsic biological traits alongside extrinsic environmental change. Whilst large mammal decline was only significantly correlated with trophic level in a multivariate GLM, it was also associated with body mass and diet under univariate analysis. Furthermore, bootstrapping plots based on broad binary cut-offs for body mass (fig. 5.8), trophic level (fig. 5.9) and diet breadth (fig. 5.10) also showed significant differences between the two groups within each set. Thus species that had a large body mass, were herbivores and which had a more complex diet, were associated with increased range declines and vice-versa. These traits appear to be linked and therefore it is surprising that VIF scores were so low, although it has been suggested that scores as low as two or three could indicate collinearity, depending on the model (Zuur *et al.* 2010).

However, the significance of trophic level did offer interesting insights into past extinction drivers. For example, it explicitly highlighted that many large herbivores declined prior to carnivores, a pattern not previously acknowledged, since large carnivores are generally regarded as most vulnerable to human activity in terrestrial systems (Woodroffe 2000; Ray *et al.* 2005; Dalerum *et al.* 2009). This is probably because persecution of carnivores particularly intensified in the most recent few centuries (Kratovichil 1968; Zimen 1978; Stahl and Artois 1994; Breitenmoser 1998) and was therefore well documented historically, as well as conflict continuing with humans today (Woodroffe and Ginsberg 1998). Furthermore, their major decline is occurring during a period of heightened conservation awareness,

with large carnivores a focus of current conservation attention in Europe (e.g. Kaczensky *et al.* 2013). The relatively early decline of lion and leopard in the mid-late Holocene (fig. 5.1) proved an exception to the later extinction of carnivores, but they were in fact at the edge of their range in Europe so did not represent an observed wide-scale decline, and leopard continues to persist in the Caucasus and parts of Russia (Khorozyan and Abramovich 2007), for which zooarchaeological evidence was lacking.

Thus overall, inadequate historical baselines may have provided an extinction filter that has obscured longer-term extinction patterns in wide-scale terrestrial systems (Balmford 1996). This has also been acknowledged as a problem at a global scale, with species that became extinct prior to the recent historical period during the Late Quaternary being excluded from global assessments of the patterns and drivers of extinction risk, consequently distorting our perception of relative patterns of extinction risk (Turvey and Fritz 2011).

Further evidence also suggests that the loss of large prey species prior to large predators in human-dominated landscapes may not be a phenomenon unique to Europe. In China, several large herbivores such as the regionally extirpated Asian elephant (*Elephas maximus*) and Javan and Sumatran rhinos (*Rhinoceros sondaicus* and *Dicerorhinus sumatrensis*), and the globally extinct (or extinct in the wild) endemic Père David's deer (*Elaphurus davidianus*), giant muntjac (*Muntiacus gigas*) and Chinese buffalo (*Bubalus mephistopheles*), disappeared from much or all of China during the Holocene before the recent historical era (Jiang *et al.* 2000; Xu 2000; Elvin 2004; Rookmaaker 2006; Turvey *et al.* in review), whilst the country's large carnivores such as tiger (*Panthera tigris*), leopard (*Panthera pardus*) and wolf (*Canis lupus*) survived across much of this large region into the very recent historical era or even up to the present day (Coggins 2003; Tilson *et al.* 2004; Smith *et al.* 2010). Similarly, in the heavily populated Near East (the so-called 'Cradle of Civilisation') wild ungulates such as hartebeest (*Alcelaphus buselaphus*), aurochs (*Bos primigenius*) and hippopotamus (*Hippopotamus amphibius*) are also documented as disappearing during the Iron Age (Tsahar *et al.* 2009) whilst its large carnivores persisted either up until the recent historical period or the present day (Wilson *et al.* 2009; Schnitzler 2011).

Relative decreases in prey abundance have been found to result in proportionally greater declines of large carnivores (Carbone *et al.* 2011), thus herbivore declines preceding carnivore declines often by centuries or even millennia at a local scale appear counterintuitive. However, during the early Holocene the domestication of pigs, sheep and cattle across Europe (Götherström *et al.* 2005; Larson *et al.* 2007; Peter *et al.* 2007) would have provided a relatively accessible new prey base for many carnivores such as wolf and lynx in the absence of an abundant wild prey base (Breitenmoser 1998). Furthermore, introductions of prey species such as fallow deer, rabbit and hare across Europe all the way up to the UK and Scandinavia during the Late Holocene (Yalden 1999; Sykes 2004; O'Connor and Sykes 2010) would also have provided a substitute for native prey loss. Although no relationship was found between large mammal decline and home range, carnivores have been shown to have

higher maximum natal dispersal distances than herbivores (Whitmee and Orme 2012) meaning that carnivores may have been able to better exploit the landscape and maintain wider geographic ranges in the face of changes to their environment.

5.6 Conclusion

Zooarchaeological data is an extremely useful, but currently underused, source of information on past distributions of both extinct and extant species. Despite biases associated with this type of data, bootstrapping proved an effective method to identify range declines of several large mammal faunas independent from sample size effects. Efforts should be made to incorporate as long term data as possible into wide-scale analyses of extinction dynamics in order that already extinct populations and species are not excluded, thereby distorting our understanding of extinction processes and extinction risk across taxa.

Chapter 6. Historical determinants of regional persistence of large mammals and lessons from long-term datasets

6.1 Abstract

A substantial body of research has previously investigated the major factors influencing current day global patterns of extinction and extinction risk; however, such studies have generally been limited to assessments based on extant, often depauperate, faunas, thus excluding information on species which have experienced wide-scale historical declines. Here, I compiled regional last occurrence data from zooarchaeological, historical and ecological datasets in order to reconstruct patterns of extirpation and persistence for large mammal species across Europe throughout the Holocene. Using information on both extinct and extant representatives of faunas uniquely allowed for the identification of the key intrinsic and extrinsic factors that have determined survival through time, rather than at one static point. Mammals with a higher body mass were more likely to have experienced regional extirpation, and countries with a higher human population density (HPD) and lower average elevation were more likely to have lost their large mammal faunas. In general species varied in their tolerance to HPD but, for the first time, it was demonstrated that there was an overall significant negative relationship between a species' body mass and the HPD at which it could persist. In Europe, current-day conservation management means that large mammals can now survive in areas of high HPD that they were not able to withstand historically. However, these results on individual species' tolerances to HPD have important implications for the conservation of related but vulnerable large mammal faunas on other continents that are threatened by rapidly growing human populations.

6.2 Introduction

The study of the Holocene fossil and zooarchaeological record has increasingly revealed unparalleled levels of biodiversity loss and ecosystem alteration as a result of human activity (Turvey 2009a). The previous chapter investigated the potential of the zooarchaeological record for revealing continental-level patterns and processes of mammalian extinction that took place prior to historical memory where the major source of reliable available evidence for reconstructing past biodiversity loss was bone assemblages from archaeological sites. However the zooarchaeological record was found to be less informative across wide geographic areas for the last five hundred year period, where quantity of data rapidly declined. Thus it failed to document historical-era declines between the Late Medieval and present day for species which only declined during the last five hundred years and during a period where human impacts not only continued, but accelerated into the industrial era through to the present day (Steffen *et al.* 2011). Patterns of historical mammal extinctions have therefore so far gone undocumented for Europe and also have yet to be combined with data from older time periods. Therefore in order to be able to fully reconstruct extinction patterns for the European Holocene period,

the zooarchaeological record needs to be supplemented by other forms of evidence which document the recent past, such as the historical record and modern-day ecological datasets.

However, each type of evidence has its benefits and limitations which must be considered both when combining such data and also in subsequent interpretation, due to the so-called 'epistemological gap' between data from the past and present (Turvey and Cooper 2009). Thus zooarchaeological data can be used to reconstruct wide temporal, geographic and taxonomic patterns of extinction but their temporal resolution is generally constrained, whilst historical evidence can often reveal more specific information on the timings and drivers of declines particularly for recently extinct species. Data on extant threatened species can then provide insights into the final stages of extinction including population and range collapse and their proximal drivers. Indeed, palaeontologists and zoologists are often asking the same questions of their relative datasets, be they based on ancient or modern information, but answer them by working in artificially constructed temporal silos according to availability of particular types of evidence, when they could often be working more closely together. Whilst the differences between these datasets should be recognised, opportunities to integrate them need to be embraced and developed (Swetnam *et al.* 1999; Dietl and Flessa 2011).

Using multiple lines of evidence would then facilitate through-time analysis of both the extinction and survival of populations of species, rather than being restricted to studying extinction dynamics of either extinct or extant faunas, as is currently the case in palaeontology and ecology. The results of Chapter 5 indicated that large mammal declines were unique in their trajectories across species, but zooarchaeological data only reliably extended to the Late Medieval and therefore could not include either more recent extirpations or information on species which experienced no decline. Reconstructing patterns of both Holocene extinction and survival could therefore improve our understanding of the long-term responses of large mammals to human pressures and to identify whether these were indeed species-specific or displayed common patterns across assemblages.

6.2.1 Mechanisms behind extinction patterns

Understanding the factors that drive species to extinction is crucial for implementing strategies to halt such declines and to predict where future conservation funds may need to be targeted. It is now well recognised in both the palaeontological (Martin 1984; Lyons *et al.* 2010; Roy *et al.* 2011) and ecological (Purvis *et al.* 2000a, Van Allen 2012) literature that not all species are equally prone to extinction. Taxonomic and phylogenetic extinction patterns have also been identified for global Holocene mammal faunas (Turvey and Fritz 2011). However, whilst such studies are important for understanding the general ecological mechanisms underlying extinction, they may be of limited practical use, particularly in conservation. As studies have generally been focused on extinction correlates of broad taxonomic groups (e.g. entire classes or orders) and at wide spatial scales (usually global), it is unclear whether the results could be applied to identify species at risk within specific geographical regions or assemblages of species. Thus, in terms of targeted conservation intervention and management, understanding taxon-, region- and threat-specific correlates of declines

might be more powerful than identifying patterns across extremely broad categories (Fisher and Owens 2004).

Furthermore, studies on the intrinsic and extrinsic correlates of extinction to-date have been limited to assessing correlates of extinction vulnerability in surviving representatives of mammal faunas (Cardillo *et al.* 2005; Cardillo *et al.* 2008) despite indications that historical human impacts may have affected patterns of extinction and persistence (Fritz *et al.* 2009; Turvey and Fritz 2011). Using current day assessments of extinction risk as indicators of vulnerability are inherently biased, as they exclude both prehistoric and historical extinctions and fail to account for recent conservation management that has improved the status of some species despite past declines. For example, European bison (*Bison bonasus*) became extinct in the wild in the early twentieth century due to human pressures (Pucek *et al.* 2004) but has since been recovered from captive populations and is now only listed as Vulnerable (Olech 2008). Instead, a better indicator of true threat potential might be to use extinction itself, i.e. information on past extirpations (and persistence) up to the present day, rather than the biased assessment of remnant, surviving, and often, as a consequence, more resilient populations that may not be representative of the species as a whole.

6.2.2 Human population

Human population growth has been a topic of interest ever since Thomas Malthus's famous essay in 1798 warning of the dangers of rapid rises in population, concerns which have since spread beyond the realm of economics into natural resource use, sustainability and biodiversity conservation. Humans have been implicated in the two most recent global extinction episodes: i) the so-called 'megafaunal extinctions' at the end of the Pleistocene, and ii) the current extinction crisis. Whilst the relative contributions of humans and climate change have been extensively debated with regards to the former (e.g. Koch and Barnosky 2006; Lorenzen *et al.* 2011), humans are incontrovertibly responsible for driving recent global species declines and extinction through hunting, habitat degradation, the introduction of non-native species and now even climate change. Indeed human impacts on the Earth's natural systems over the past two hundred years have been so rapid and widespread, as to warrant the proposal of a new geological epoch, the 'Anthropocene' (Crutzen 2002; Steffen *et al.* 2011; Zalasiewicz *et al.* 2011). However, the number of documented species extinctions between these two infamous extinction episodes during the majority of the Holocene epoch is now understood to be far higher than previously assumed and growing (Turvey 2009c) and we increasingly need to revise assumptions that pre-industrial era human activity was not a driver of species-level extinctions.

The majority of research into Holocene human impacts on ecosystems has taken place on island faunas, principally because where human arrival has been documented and dated in ecologically simple systems that often lack other large mammalian predators, it has been easier to draw causal links between human colonisation events and subsequent species extinctions (e.g. Steadman *et al.* 1984; Burney *et al.* 2003; Turvey *et al.* 2007; Bromham *et al.* 2012; Duncan *et al.* 2013). However, at

the continental level, Holocene extinction chronologies have generally been more difficult to associate with anthropogenic activity due to the longer and more complex history of human occupation and cultural development in these areas. Indeed the longer co-evolution between humans and animals has been proposed as an explanation for the survival of large-bodied mammals in Africa (Martin 1984). Likewise in Europe, which has been colonised by hominins for over half a million years (Roebroeks 2006), humans were unlikely to represent a novel predator during the Holocene. Furthermore, ongoing and repeated waves of cultural and technological development that fuelled population growth spread unevenly both spatially and temporally across Europe (Milisauskas 2011), making it extremely difficult to tease out patterns and drivers of species loss, in comparison with simple island systems.

However, the Holocene Epoch does have the advantage of being a period of relative climatic stability, changing little from the end of the Younger Dryas to the Industrial era (Davis *et al.* 2003), and Holocene climate change has yet to be incontrovertibly associated with any global species-level extinctions. Furthermore, whilst Europe had already been colonised by humans for several hundred thousand millennia, populations were generally low during the variable and often harsh conditions of the Late Pleistocene (Boquet-Appel *et al.* 2005). Thus, facilitated by an ameliorated climate, human technological progression with associated population growth, only substantially accelerated during the Holocene (McEvedy and Jones 1978). Therefore whilst regional variation in climate across Europe must be taken into account in driving small-scale environmental change, broad-scale impacts on biodiversity can be more easily associated with human activity. Indeed, there are no documented Holocene extinctions that have not been attributed to a human-induced cause (Caughley 1994; Turvey 2009b).

Human population density (HPD) is a commonly used proxy for anthropogenic impact, particularly where more detailed information on the specific effects of different types of human activity cannot be obtained or easily quantified (e.g. Thompson and Jones 1997; Woodroffe and Ginsberg 1998; Woodroffe 2000; Cardillo *et al.* 2004). Such studies have also generally focused on the effect of human population in relation to carnivores, where direct persecution is known to have taken place. During the Holocene of Europe however, the principal disturbances to ecosystems would probably have been both direct hunting and habitat conversion and the impact would have been felt across a wider range of species. The detailed zooarchaeological record of Europe attests to the prolific hunting of mammals across the Holocene, from the Mesolithic, when this would have been the principal mode of biodiversity exploitation, up to the Late Medieval, when it increasingly also became both a social and political activity (Benecke 1999a; Yalden 1999; Allsen 2006). However the palynological and archaeological records also show extensive evidence for the deforestation of large areas of Europe in order to cultivate plants and graze livestock, as well as to provide areas for increasingly large permanent human settlements that domestication was supporting (Williams 2000; Kaplan *et al.* 2009). Habitat fragmentation would in turn have facilitated an increase in hunting pressure by opening up forests and improving access for hunters, making these two factors difficult to tease apart in terms of

their relative impact on species extinctions. Introduced species were also a major source of species loss across the Holocene at a global level, but these effects were generally more severe on islands than large continents and on birds than mammals (e.g. Turvey *et al.* 2007; Lockwood *et al.* 2009; Turvey and Fritz 2011).

Thus, whilst HPD is not a precise reflection of human impact, it is nonetheless a reasonable proxy and also has the benefit of being a standardised measure with which to compare across broad spatial scales and between a range of species. Furthermore, there is already a body of ecological evidence associating HPD with patterns of large mammal persistence or extirpation (e.g. Cardillo *et al.* 2004; Cardillo *et al.* 2008; Karanth *et al.* 2010).

Most studies have focused on the effects of spatial variation in HPD on biodiversity but there are few, if any, analyses to date that have examined the effects of temporal variation in HPD on biodiversity, yet which could 'offer a particularly rigorous examination of the threats humanity poses to conservation' (Luck 2007). Moreover, there is unique potential in using long-term data on species extinction and survival to identify mammalian responses to human impacts through time and more specifically, whether there are critical threshold levels of HPD that different species can tolerate. The outcome of such an analysis may then be able to provide genuine predictive power for identifying generalised versus species-specific patterns of decline or persistence across the European large mammal fauna.

This chapter therefore reconstructs through-time patterns of Holocene regional extirpation and survival across Europe's large mammal assemblage up to the present day. This dataset is then used to assess intrinsic and extrinsic factors relating to the loss of populations as well as entire species. Finally I compare this dataset with information on past HPD across Europe to identify critical HPD thresholds for large mammal persistence, in order to identify whether human impacts across the Holocene have affected species equally or whether they have responded individually.

6.3 Methods

6.3.1 Last occurrence data

In order to research historical extinction drivers and to identify correlates of species presence/absence across Europe over time, accurate data on regional extirpation dates were needed. As regional extirpations occurred throughout the Holocene, information on the temporal occurrence of the last known individuals or populations of different species were compiled from zooarchaeological, historical and current-day literature for each country of Europe up until the year AD 2000 (see Appendix 5 for a list of all references). All data were collected at the country level as this was the highest spatial resolution that could be maintained consistently across species given the quality and quantity of regional data. Furthermore, the specific drivers of historical population declines across

Europe were often dictated by the socio-political context within country borders (for example, concerted government-driven extirpation programmes, and human population). Therefore to try to even out or interpolate spatial patterns of extirpation would have likewise flattened and homogenised variation in the very human drivers of extinction that were being measured.

The species included were as stated in Chapter 2. Only native established populations were included in data collection and the earliest known extirpation date for each species in each country was taken. Data resolution ranged from specific calendar dates recorded in the recent historical literature for the deaths of the known last individuals of regionally extirpated species (e.g. death of the last known aurochs (*Bos primigenius*) in Poland in 1627), to the last known appearance of species in the zooarchaeological record associated with broader time intervals. Whilst many recent historical dates are likely to be reasonably reliable, with some almost certainly representing the true date for death of the final individual of a species within a region, the majority of older historical and zooarchaeological dates were interpreted as a *terminus post quem* preceding final extinction rather than an absolute extirpation date, due to the Signor-Lipps effect (Signor and Lipps 1982). Where there was more than one zooarchaeological date, the most recent directly dated record was favoured. Where there was no recorded disappearance of a species from a country it was noted as 'extant'. Reintroductions and natural recolonisations of species after extirpations were not counted as representing modern-day occurrence data, likewise vagrant individuals and populations were also excluded unless there was reasonable evidence for establishment and/or breeding of populations by AD 2000. For example golden jackal (*Canis aureus*) had been intermittently recorded in Germany and the Czech Republic but with no sightings or firm evidence for established populations since the 1980s, so these countries were excluded from the species' extant range, whereas vagrant populations in Italy, Ukraine and Austria did appear to have established in the past few decades so were included in the species' extant range (Arnold *et al.* 2012). Where extinction-date information for a species was uncertain, data for those countries was omitted from the analysis. For example, patterns of past occurrence and the timing of extirpation of wild horse (*Equus ferus*) across many countries of central Europe are very poorly understood due to confusion over its identification with the domestic horse in the zooarchaeological record (Robert Sommer, Christian-Albrechts-Universität zu Kiel, personal communication, 2010; see Appendix 1), and so data for these countries were excluded from the analysis.

6.3.2 Life history correlates of mammalian extirpations

In order to assess intrinsic correlates of mammalian extirpations in Europe, the number of countries in which a species was either extant or had become extinct by the year AD 2000 was noted using the last occurrence database and the proportion of occupied countries calculated. The following life history variables were then assessed for their relationship to the proportion of occupied countries across a species' historical range: body mass, diet breadth, trophic level, interbirth interval and litter size (see Chapters 3 and 4 for specific information on variables). As per Chapter 3 and following

Bielby *et al.* (2007), the reproductive variables of interbirth interval and litter size were chosen to capture two orthogonal axes of life-history covariates across mammals related to timing and reproductive output respectively. Data for *E. hemionus* from PanTHERIA (Jones *et al.* 2009) were used as a proxy for the closely related (possibly conspecific) extinct *E. hydruntinus*; sources for all other ecological data have been described in Chapter 3. Body mass was logarithmically transformed for analysis.

Individual regressions were first carried out to identify significant variables to put forward into the maximal model. The relationship between these predictor variables and proportion of countries occupied for each species were then analysed using analysis of covariance (ANCOVA) with binomial errors to account for the response variable being a proportion and the explanatory variables representing a mixture of continuous and categorical. Model simplification was undertaken using chi-squared tests to assess for increases or decreases in scaled deviance resulting from removal of terms from the model. Overdispersion (extra unexplained variance) in the multiple regression was accounted for using quasibinomial errors.

The shared ancestry of species means that, due to the possible similarity of traits between close relatives, species cannot necessarily be treated as statistically independent units. If the response variable in a model is an inherited trait then phylogeny of species should be included to account for the non-independence. The response variable here is based on loss of geographic range of a species and it is debatable whether this would be affected by phylogeny. On the one hand geographic range generally displays weak phylogenetic signal (Diniz-Filho and Torres 2002; Webb and Gaston 2003; Jones *et al.* 2005; Webb and Gaston 2005; Freckleton and Jetz 2009), although this has been debated (Hunt *et al.* 2005; Waldron 2007), but on the other hand range loss is one of the criteria used to assess extinction risk, a trait which does carry a phylogenetic signal (Purvis 2008). However, in general species phylogenies can only be used with linear models; therefore in this case the best option was to include order and family as variables in the ANCOVA to see whether there was a phylogenetic signal in the response variable. However, as there were 10 families within the dataset, the sample size of only 30 species was insufficient to run an interaction model and there was also a danger of model overfitting for an additive model, and so only order was included.

6.3.3 Extrinsic correlates of mammalian extirpations

In order to assess extrinsic correlates of mammalian extirpations in Europe, the number of extant and extinct large mammal species at the year AD 2000 was noted for each country using the last occurrence database and the proportion of species lost was calculated for each country. The following explanatory variables were then assessed for their relationship to the proportion of species lost in each country: human population density (HPD); % forest cover, average elevation of a country, Gross Domestic Product (GDP) and coast/area ratio. All variables were calculated at the time point AD 2000. HPD, average elevation and GDP were all log transformed for analysis.

Information on HPD and GDP were obtained from the World Bank (2013) and the Office for National Statistics (ONS 2013) websites. Percentage forest cover data were taken from the Food and Agricultural Organisation (FAO 2013) and the UK Clearing House Mechanism for Biodiversity (2013) websites. In order to calculate average elevation for each country, a high-resolution 30-arc seconds (c.1km) elevation map was downloaded from the WorldClim database (2012). This was clipped to a map of the European countries being investigated and zonal statistics were used to calculate the summed elevation values of each grid cell for each country. This was measured as metres above or below sea level, as a positive or negative integer respectively. This value was then divided by the country area (km²) obtained from the World Bank (2013) to give the average elevation for each country. Coast/area ratio was calculated using data on the length of coastline for each country, obtained from the CIA World Factbook (2012), and again divided by the area (km²) of the country, obtained from the World Bank (2013).

Analysis and model simplification were performed in the same manner as the analysis of life history drivers above, but here regression, rather than analysis of covariance, was performed to account for all explanatory variables being continuous.

6.3.4 Human population density

The aim of the final analysis was to identify differential effects of HPD at the species level and to identify critical human density thresholds for different species. Temporally the analysis concentrated on country-wide extirpations throughout the Holocene with a cut-off date of AD 2000. Human population figures for AD 2000 were taken from the World Bank (2013). Information on Holocene human population was principally obtained from McEvedy and Jones (1978), which estimated human population numbers at a regional level across Europe from around the Mesolithic to the present day. This data source broadly dealt with geographical regions of Europe as defined at the time of publication, therefore some countries, such as Ukraine, Belarus and the Baltic States were subsumed under larger geo-political areas. Past human population estimates for these countries were therefore obtained from additional sources (Lahmeyer 2006; Zarina 2006; Estonian Institute for Population Studies 2013). Individual country information could not be obtained for the Czech Republic and Slovakia separately, therefore relative human population was estimated at AD 2000 for both countries and back-projected onto overall human population numbers given for Czechoslovakia in McEvedy and Jones (1978) to estimate human population for the respective countries. Whilst this did assume constant relative population levels back in time, there was little reason to suspect substantially different growth rates in historical population and doing so allowed for a higher spatial resolution for analysis. Conversely, very small countries were joined with larger related countries in order to minimise spatial bias; for example, Luxembourg into Belgium; Liechtenstein into Switzerland; Moldova into Romania; and England, Scotland and Wales into Great Britain. Accurate historical population estimates for the countries making up former Yugoslavia could not be obtained, therefore data for Bosnia and Herzegovina, Croatia, Macedonia, Montenegro, Serbia and Slovenia were conflated. For the same reason Armenia, Azerbaijan and Georgia were subsumed into the Caucasus region. Finally,

all human population estimates were converted to HPDs (people per km²) using country area data from the World Bank (2013) and compiled in a database.



Figure 6.1 Map of the countries of Europe as defined for the analysis of critical thresholds of human population density.

For each species, four historical points in time were selected that covered the temporal range associated with its past extirpation and for which HPD information was available. This included the nearest time point to both the earliest and most recent regional extirpation for a species, and two evenly spaced time points in between. Whilst this necessarily resulted in different time periods being selected across species, it was important to capture the variation in tolerance to different HPDs, as regional extirpations of different species were temporally non-congruent. In general, temporal resolution increased concurrently across both the HPD and the last occurrence datasets, (e.g. 'Neolithic', '1500s', '1950') meaning that there was never a wide disparity in the precision of a last occurrence date and the equivalent available HPD data. The species' presence or absence (1,0) was then noted from the last occurrence database within each country along with the corresponding HPD at each time point. The effect of HPD on presence/absence data was analysed using binary logistic regression, a widely accepted method for analysing binary data (Crawley 2007). In order to assess model fit in a maximum likelihood model, change in residual deviance between the null model and the fitted model was observed in the form of a chi square distribution. This analysis was carried out for 22 out of the 30 species that experienced regional extirpations.

In order to incorporate temporal patterns of extinction associated with HPD using logistic regression, it necessarily involved ‘sampling’ each country four times. This could be considered pseudoreplication, i.e. multiple observations from a single replicate or sequential measurement of multiple observations on the same treatment replicate (Millar and Anderson 2004), thus violating assumptions of independence of data points and artificially inflating the sample size. The general danger is that this increases the potential for Type 1 errors (the incorrect rejection of a true null hypothesis). However, using historical data constrained the variety of methods available for temporal analysis and methodological limitations were considered in the application and interpretation of the analysis throughout. In this case, only when a species had disappeared from a region did subsequent non-independence of points occur, i.e. once a species had become extinct, it was necessarily extinct in all subsequent time periods, whereas being extant in one time period did not affect the outcome of its presence or absence in subsequent time periods. Additionally, in order to assess the cumulative pressure of HPD over time, it was the very process of repeatedly sampling the same area that was required, and the effect of change in HPDs could not be calculated as precisely using one time period only. Furthermore, the null hypothesis (no association between HPD and presence/absence) was accepted 9 times out of 22, 41% of the time, suggesting that the model did not erroneously increase Type 1 errors.

For some species there was a concern that there may have been insufficient variation in the response variable to reliably detect a relationship between species presence and HPD, for example for species that experienced very few regional extirpations and did so more recently, such as roe deer (*Capreolus capreolus*) and otter (*Lutra lutra*). Therefore a minimum recommended sample size was calculated for each species using the metric ‘number of events per variable’ (EPV), following Peduzzi *et al.* (1996) for logistic regression analysis. EPV was calculated using the simple equation:

$$N = 10k / p$$

where k was the number of covariates or independent variables (in this case only 1, HPD) and p was the smallest of the proportions of negative or positive cases in the population, i.e. whichever was the lowest proportion of 0s or 1s for each species. The recommended EPV was noted alongside each species after analysis in order to help interpret the strength of results.

Where there was a positive association with HPD for a species, a ‘critical human population density’, i.e. the point at which populations of the species were predicted to be extirpated, was calculated from the logistic regression models. This was calculated at a probability of 50%, as this is analogous to a measure of LD₅₀ (lethal dose₅₀), the dose of a drug that kills exactly 50% of experimental subjects, and has been used as an accepted threshold in previous studies of the relationship between human population density and species loss (Woodroffe and Ginsberg 1998; Woodroffe 2000).

In order to assess whether there was a general relationship between critical HPD threshold and body mass across all species, body mass was regressed against critical HPD thresholds where these were calculated for a species. However, this omitted data for the species for which there was no relationship between HPD and persistence, and also for the 8 species which did not suffer any historical extirpation. Therefore in order to be able to include all species, a second analysis was carried out which took the average HPD across the extant historical range of all species. This time, four standardised time periods were chosen across all species (AD 0, AD 1000, AD 1500 and AD 1900) which broadly captured the temporal range of the majority of regional extirpations. Average HPD was then calculated for each species across its range for these four time periods when it was present (i.e. only at all the '1s') and this was then regressed against body mass. By using presence data only, all species could be included in the analysis. A phylogenetic generalised least square (PGLS) was then run in order to check whether there was a phylogenetic signal in the response variable (HPD at which a species was either present or absent). As no signal was detected, both analyses were carried out using straightforward linear regression.

6.4 Results

In all, 279 country-wide extirpations were recorded from Europe during the Holocene, of which 187 were for herbivores and 89 for carnivores.

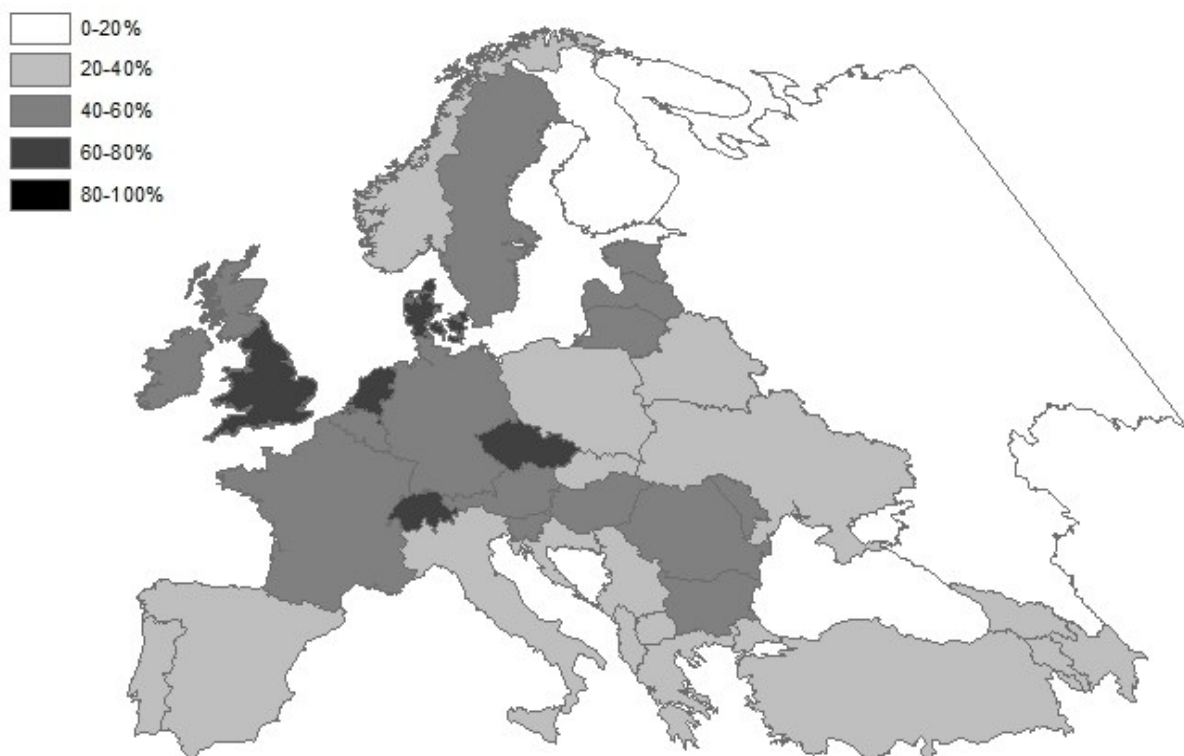


Figure 6.2 Map of Europe showing percentage of large mammals extirpated from each country during the Holocene.

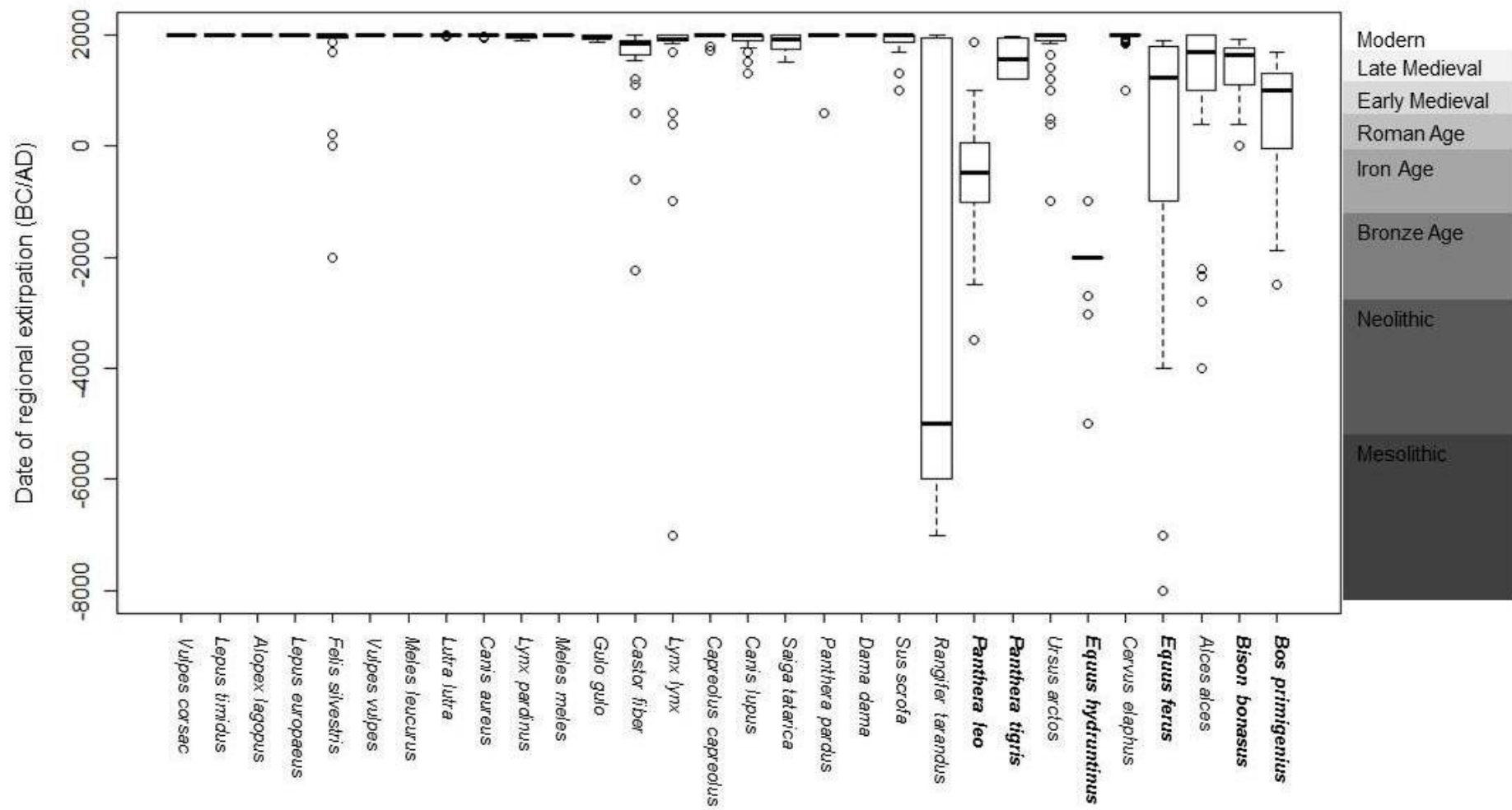


Figure 6.3 Temporal extirpation patterns for all European large mammals for the Holocene Epoch. Dates are shown both in calendar years (left) and in archaeological periods (right). Each point denotes a regional (country-level) extirpation. Extant species are denoted at the point AD 2000. Species are ordered by body mass with the smallest on the left and largest on the right. Species in bold are regionally or globally extinct from Europe. European bison was treated as extinct due to its extinction in the wild; its current extant status is due to reintroduction from captive populations into protected areas (Pucek 2004).

6.4.1 Life history correlates

The proportion of species range loss was significantly positively related to body mass, and negatively related to both trophic level and litter size under univariate analysis (see Appendix 6). It was not significantly related to either diet breadth or interbirth interval. However in the multivariate model only body mass was significantly positively related to the proportion of range loss (Table 6.1). Whilst order was also retained in the multivariate model, only one factor level containing one species (Castoridae) was significant, and so the overall phylogenetic signal was interpreted as being weak or not present.

6.4.2 Extrinsic correlates

The proportion of species lost in each country was positively associated with HPD, and negatively related to forest cover and average elevation (see Appendix 6). It was not significantly related to either GDP or coast/area ratio. However, only HPD and average elevation were retained as significant factors in the multivariate model (Table 6.1).

6.4.3 Human population density

At the species level, extirpations of 13 out of 22 large mammal species were significantly associated with HPD (Table 6.2, fig.6.4) and for which critical thresholds were calculated (Table 6.2). Body mass was found to be significantly negatively associated with both critical HPD thresholds and average HPD across species' historical ranges (Table 6.1; figs. 6.6, 6.7).

Table 6.1 Results of the minimum adequate binomial GLMs showing: i) the significant intrinsic factors relating to the proportion of range lost for each species; ii) the significant extrinsic factors relating to the proportion of species lost for each country; and results of the linear regressions showing: iii) relationship between body mass and critical human density thresholds calculated from logistic regressions; and iv) relationship between body mass and average human population density across a species' extant historical range.

	a	SE	t - value	
Intrinsic factors				
(Intercept)	-8.383	2.524	-3.322	**
Log (body mass)	0.693	0.205	3.375	**
Order (Rodentia)	3.287	1.298	2.532	*
Extrinsic factors				
(Intercept)	0.625	0.884	0.707	
Log (HPD)	-0.366	0.128	-2.848	**
Log (average elevation)	0.228	0.093	2.456	*
Critical human population density				
Intercept	10.926	2.488	4.391	**
Log (body mass)	-0.683	0.216	-3.170	**
Average human population density				
Intercept	32.647	6.836	4.776	***
Log (body mass)	-1.856	0.645	-2.877	**

* p < 0.05, ** p<0.01, *** p<0.001

Table 6.2 Results from logistic regressions of species persistence and human population density

Species	Body Mass (g)	Time points	Number of countries within historical range	Number of countries extirpated from	Recommended Events Per Variable (EPV)	Change in deviance	Critical human density (people per km ² ± S.E.)
<i>Vulpes corsac</i>	2615	E	1	0			
<i>Lepus timidus</i>	3105	E	19	0			
<i>Alopex lagopus</i>	3584	E	4	0			
<i>Lepus europaeus</i>	3816	E	27	0			
<i>Felis silvestris</i>	4573	AD 0, 1000, 1500, 1750	31	11	44	3.1	Not calculated
<i>Vulpes vulpes</i>	4820	E	32	0			
<i>Meles leucurus</i>	6250	E	1	0			
<i>Lutra lutra</i>	8869	AD 1925, 1950, 1975, 2000	32	2	500 [†]	7.8 **	531.5 (± 1.5)
<i>Canis aureus</i>	9659	AD 1925, 1950, 1975, 2000	13	1	250 [†]	2.6	Not calculated
<i>Lynx pardinus</i>	11050	AD 1850, 1900, 1950, 2000	3	1	40	2.7	Not calculated
<i>Meles meles</i>	11884	E	32	0			
<i>Gulo gulo</i>	12792	AD 1850, 1900, 1950, 2000	11	7	29	25.2 ***	38.1 (± 1.2)
<i>Castor fiber</i>	19000	AD 1000, 1500, 1750, 1900	30	22	31	27.4 ***	36.2 (± 1.3)
<i>Lynx lynx</i>	19300	AD 1800, 1900, 1950, 2000	30	15	28	72.8 ***	77.0 (± 1.1)
<i>Capreolus capreolus</i>	22502	AD 1700, 1800, 1900, 2000	32	3	143 [†]	0.009	Not calculated
<i>Canis lupus</i>	31757	AD 1700, 1800, 1900, 1950	32	13	46	46.2 ***	86.5 (± 1.2)
<i>Saiga tatarica</i>	37734	AD 1000, 1500, 1750, 1950	4	3	37 [†]	9.4 **	14.5 (± 1.4)
<i>Panthera pardus</i>	52400	AD 1000, 1500, 1750, 2000	4	1	40 [†]	0.67	Not calculated
<i>Dama dama</i>	57225	E	1	0			
<i>Sus scrofa</i>	84472	AD 1000, 1500, 1750, 1900	31	11	67	1.0	Not calculated
<i>Rangifer tarandus</i>	109089	AD 1850, 1900, 1950, 2000	3	1	40 [†]	0.05	Not calculated
<i>Panthera leo</i>	158624	1000 BC, AD 0, 1000, 1900	9	9	40 [†]	2.6	Not calculated
<i>Panthera tigris</i>	161915	AD 500, 1000, 1500, 2000	4	4	27 [†]	7.5 **	12.2 (± 1.9)
<i>Ursus arctos</i>	196288	AD 1500, 1750, 1850, 1950	32	12	44	31.1 ***	84.2 (± 1.3)
<i>Equus hydruntinus</i>	235248	3000, 2000, 1000, 0 BC	13	13	40	21.6 ***	0.9 (± 1.2)
<i>Cervus elaphus</i>	240867	AD 1000, 1500, 1750, 2000	31	5	111	0.01	Not calculated
<i>Equus ferus</i>	403599	AD 0, 1000, 1500, 1900	14	14	24	27.9 ***	6.2 (± 1.2)
<i>Alces alces</i>	461901	AD 0, 500, 1000, 1500	24	13	44	29.3 ***	12.7 (± 1.2)
<i>Bison bonasus</i>	675877	AD 500, 1000, 1500, 1750	19	19	28	18.3 ***	12.8 (± 1.2)
<i>Bos primigenius</i>	800143	AD 1, 500, 1000, 1500	29	29	21	14.9 ***	5.6 (± 1.2)

E - extant across range

*** p<0.001; ** p<0.01, *p<0.05

† Sample size lower than recommended EPV

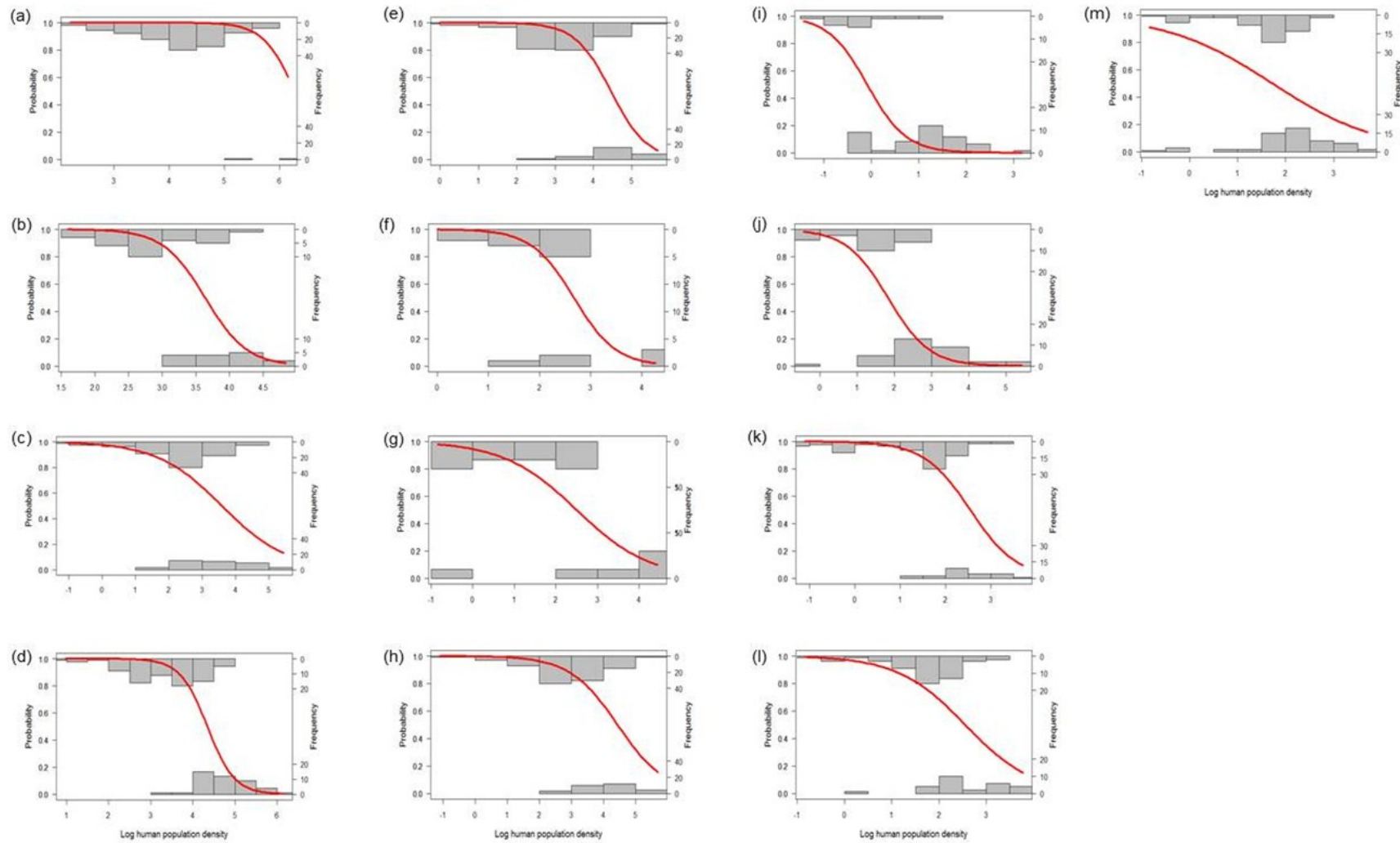


Figure 6.4 Logistic regression plots for species where there was a significant association between species persistence and human population density (measured on a logarithmic scale). Plots are presented in order of species' body mass from largest to smallest: (a) *Lutra lutra*; (b) *Gulo gulo*; (c) *Castor fiber*; (d) *Lynx lynx*; (e) *Canis lupus*; (f) *Saiga tatarica*; (g) *Panthera tigris*; (h) *Ursos arctos*; (i) *Equus hydruntinus*; (j) *Equus ferus*; (k) *Alces alces*; (l) *Bison bonasus*; (m) *Bos primigenius*.

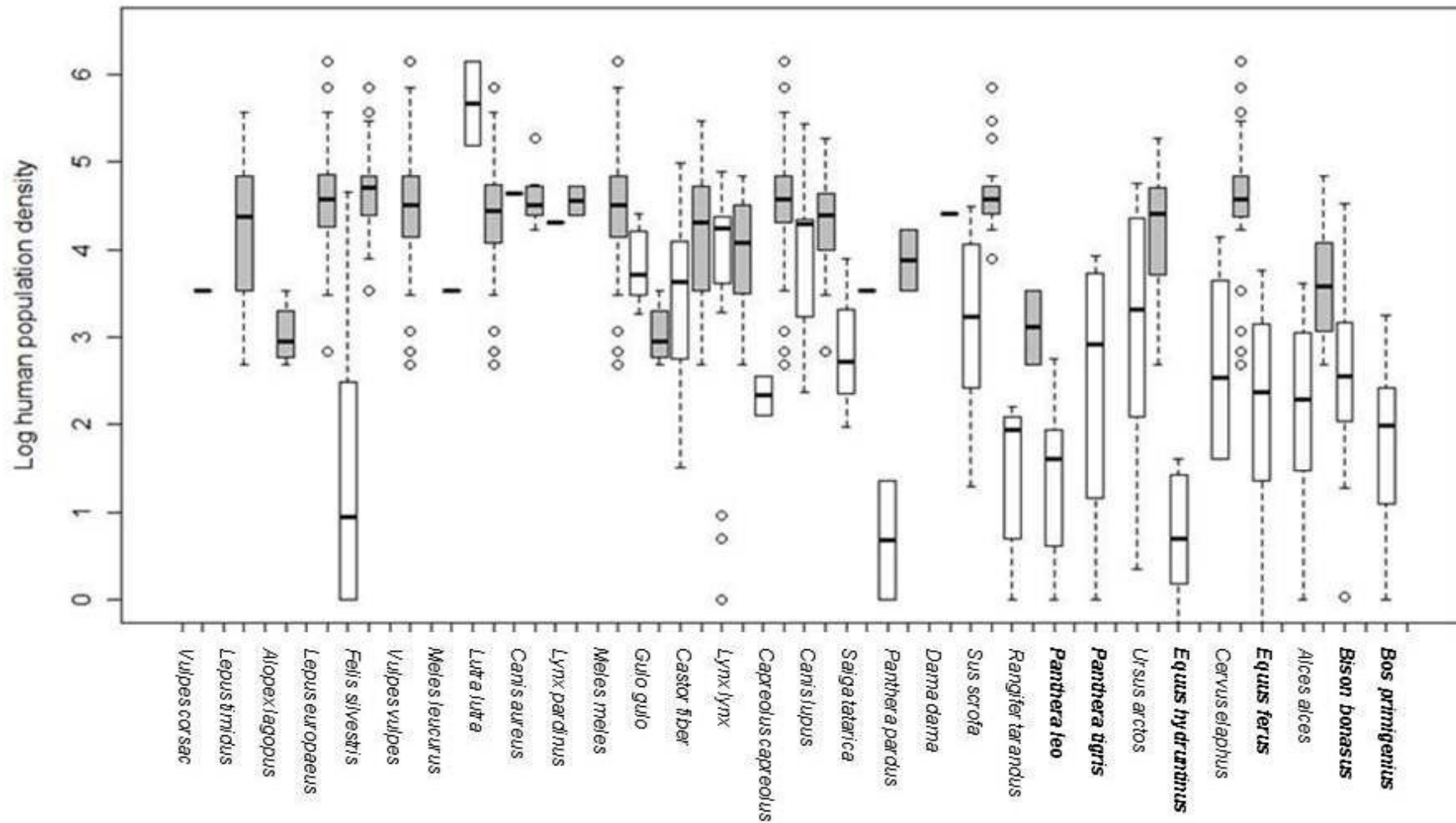


Figure 6.5 Plot of log human population density (HPD) at the point of historical regional extirpation in each country for each species (white bars) and log human population density across each species' extant range at AD 2000 (grey bars). HPD across extirpated and extant ranges are presented side by side for each species. Species are plotted in ascending order of body mass with the smallest species on the left. Species in bold have been completely extirpated from Europe so have no extant range.

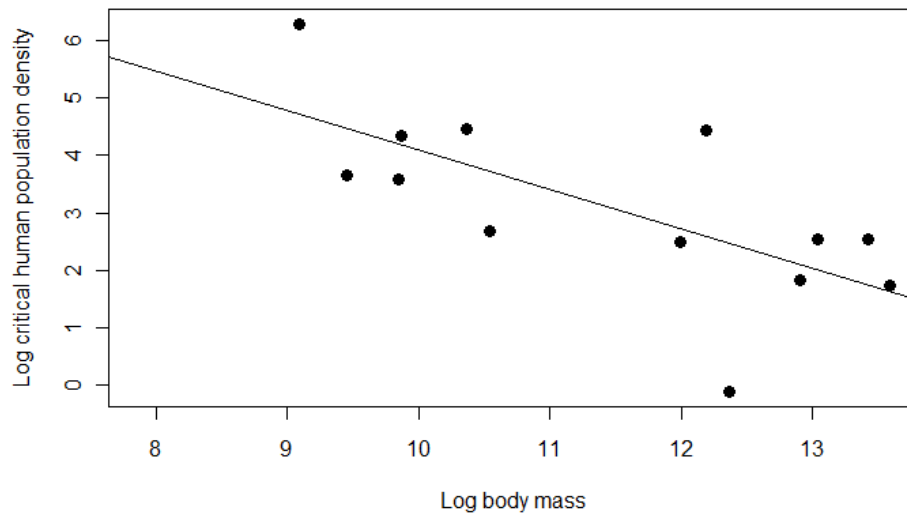


Figure 6.6 Relationship between logged body mass and critical human population density for mammal species, where this was calculated.

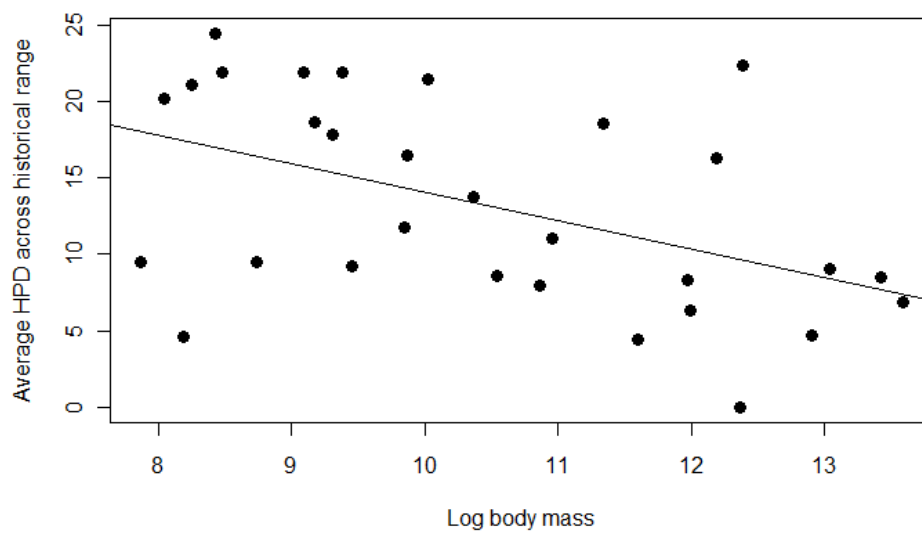


Figure 6.7 Relationship between logged body mass and the average human population density across all mammal species' historical ranges at the time points AD 0, 1000, 1500 and 1900.

6.5 Discussion

Perceptions of the severity of species declines are strongly related to spatial and temporal scale. Among the European mammal fauna, species-level extinctions have been comparatively low, with only one global continental extinction since AD 1500, that of aurochs in AD 1627 (Temple and Terry 2007). However, by constraining our focus spatially to Europe and temporally to the entire Holocene, we can add the continent-wide extinctions (in the wild) of wild ass, wild horse, European bison, tiger and lion. Honing in on regional (country-wide) Holocene mammal losses then reveals a considerable 279 extirpations, highlighting that Europe has indeed lost a substantial proportion of its large mammal fauna at regional scales. By limiting spatial and temporal definitions of extinction to those that were global and occurred after AD 1500, conservation researchers risk excluding considerable amounts of data on past mammal population losses. For example, in order to assess global mammal population loss, Ceballos and Ehrlich (2002) used the recent baseline of the nineteenth century and as a consequence, simply removed range data on pre-nineteenth century mammal extinctions from Britain from the analysis, on the basis that they would already have been exterminated from there. Given that it is precisely such extirpated populations that can reveal the 'process' leading to extinction, they should be incorporated into studies of extinction, rather than excluded. Concealing past data also distorts perceptions of the spatial distribution of extinction risk and could detract conservation focus from potentially highly biodiverse regions which have experienced elevated levels of past extinction, to those with higher current levels of diversity and threat.

6.5.1 Overall drivers of Holocene large mammal declines

Body mass is an ecological trait that is well linked to both Late Pleistocene (Martin 1984; Lyons *et al.* 2004; Koch and Barnosky 2006) and current day (Purvis *et al.* 2000b) extinction risk in terrestrial vertebrates and has also been linked to global historical declines of large herbivores (Morrison *et al.* 2007). Furthermore, impacts of both intrinsic and environmental factors increase above a body mass threshold of 3kg meaning that the largest species are particularly vulnerable (Cardillo *et al.* 2005). More recently Turvey and Fritz (2011) demonstrated for the first time that the median body mass of Holocene extinct mammals was also larger than expected under random extinction. However until now this relationship had only been confirmed for species-levels extinctions and extinction risk. The results presented here confirm that large body mass has also been a driver of increased regional-level population losses.

However this study also helps to explain current day patterns of spatial variation in the body size-extinction risk relationship, namely that large extant species at risk are almost exclusively found in the tropics (Fritz *et al.* 2009). This phenomenon is most likely attributable to a systematic extinction filter, whereby large bodied mammals have been selectively removed from temperate ecosystems prior to historical memory. This has had the effect of distorting global patterns of threat, concentrating present day mammalian extinction risk in areas that have not experienced such concerted levels of prehistoric and historical anthropogenic impact, but that are now subject to growing human pressure. Turvey and

Fritz (2011) also found that the removal of extinct species from their Holocene dataset of extinct mammals resulted in a non-significant relationship between body mass and extinction risk for southern Europe and Russia, further confirming the probable effect of an historical extinction filter in this region.

However, evidence from both palaeontology and ecology suggests that body mass-related extinction risk may not be a necessary determinant of extinction *per se* but may interact with other biological and extrinsic factors to drive extinction risk. Body mass was shown to disappear as a driver of Late Quaternary megafaunal extinctions once reproductive rate was controlled for (Johnson 2002) and Cardillo (2003) also found that among modern Australian terrestrial mammal fauna only litter size was a significant predictor once body size and phylogeny were controlled for. These results suggest that higher reproductive output may be the ultimate driver that lowers extinction rates rather than body mass, which is simply an ecological correlate of reproductive output. In this study neither litter size nor interbirth interval emerged as significant predictors of extinction, but litter size was significant under univariate analysis. A *post hoc* Pearson's correlation test between body mass and litter size also revealed that these two variables were in fact correlated ($t = -4.2977$, $df = 27$, $p < 0.001$). Thus, whilst it could not be confirmed within this study, reproductive output may underlie a species' propensity to extinction.

The relationship between body mass and extinction has also been linked to interactions with specific causal mechanisms, in this case human-mediated extinction. For example, during the late Eocene extinctions large body mass was not selected against, as the driver was global climate cooling which generally favours endotherms (McKinney 1997), and megafauna that became extinct at the end of the Late Pleistocene had survived previous Quaternary climatic cycles of cooling and warming (Lister 2004; Barnosky 2005). Cardillo *et al.* (2004) also found that whilst biological traits explained around 45% of extinction risk in carnivores, their interaction with human population density increased explanatory power to around 80%. Brook and Bowman (2005) also argued that humans produce a specific sustained mortality pressure that targets large-bodied vertebrates due to allometry, i.e. because maximal population increase is scaled negatively to body mass and generation length is scaled positively to body mass in vertebrates. This not only affirms a link between reproductive output and body mass but also suggests that large species cannot survive the continuous reductions in population that result from specifically human-related pressures. Thus body mass may not have been acting in isolation as an intrinsic determinant of extinction in this study, but was specifically exacerbated by interactions with anthropogenic impacts. The lack of signal related to phylogeny is unsurprising in this context, particularly given the relatively restricted sample size and incompleteness of the species represented within the orders included in the analysis.

The results demonstrating that historical species extirpations were associated with countries with higher HPD also support the results above, reflecting an inability for some large mammals to persist in areas of high HPD. The significant link between species extirpation and lower average elevations also

probably underlies this relationship, since humans live predominantly at moderate elevations, with populations decreasing faster than exponentially with increasing elevation (Cohen and Small 1998), thus lower elevations would be associated with higher HPD, and vice-versa. Past ranges of Holocene large mammals indicate that most species were widely distributed across lowland areas of Europe (see Chapter 5). However, many of Europe's largest mammals have now been extirpated from these regions and in central and western Europe they survive primarily in upland areas (Mitchell-Jones *et al.* 1999). Persistence of threatened species in often suboptimal habitat at high elevations appears to be a typical pattern of wider dynamics of extinction and survival. Fisher (2011) analysed the locations of 67 mammal species that had been rediscovered following disappearance and found that species that were not restricted by a small elevational range had experienced an average up-slope shift of 35%. Laliberte and Ripple (2004) also found that cougar, elk and Dall's sheep lost a large proportion of their historical range in lowland areas of North America and had shifted their distributions to upland areas. Given human demographic patterns associated with altitude, large mammals are clearly persisting where they are most likely to avoid conflict with humans. However, it should be noted that, as future climate change makes regions of lower elevation increasingly hazardous for human habitation (McGranahan *et al.* 2007) and potentially increases the climatic suitability of higher elevations for humans, montane areas may cease to provide refuge for Europe's large mammals if they and the species within them are not sufficiently protected (e.g. Morueta-Holme *et al.* 2010).

Yet these pressures may not have affected all species equally. Several species experienced extirpations relatively early on in the Holocene (fig. 6.3) which may have been unrelated or only indirectly related to human pressures. For example reindeer (*Rangifer tarandus*) was extirpated in the very early Holocene in the Baltic region and southern Scandinavia principally due to rapid postglacial climate change (Ukkonen *et al.* 2006), whereas the forest subspecies (*R. t. fennicus*) was driven to extinction by hunting in the early 1900s (Ruusila and Kojola 2010). Extirpations of some large mammals also occurred earlier on insular regions of northwestern Europe (e.g. Britain, Ireland, Denmark, southern Sweden) than on mainland areas of Europe, presumably due to their isolation and smaller, disconnected populations that made them more vulnerable to both human and stochastic pressures. For example lynx (*Lynx lynx*) became extinct in Ireland in the early Holocene, and was evidently rare in any case since there is only one known record from this country (Woodman *et al.* 1997). Wild horse also disappeared from Britain, Denmark and southern Sweden in the early Holocene (Lepiksaar 1986; Yalden 1999). Several other species experienced early extirpations from these regions in the mid Holocene such as lynx, wildcat (*Felis silvestris*), beaver (*Castor fiber*), bear (*Ursus arctos*) and elk (*Alces alces*). It is noteworthy that the range of European bison did not extend as far northwest into these areas and its first regional extirpations are not recorded until slightly later around the Roman Age (fig. 6.3).

Whilst there was no statistically significant trophic level effect on species persistence in the full multivariate model, there is some observational evidence to suggest that broad taxonomic groups may have had differential survival rates related to elevation. For example, Italy, Austria, Switzerland

and Spain have all retained large carnivore populations (Kaczensky *et al.* 2013) in some form in their mountain ranges, yet large herbivores such as aurochs, European bison, elk and wild horse have not survived in these countries at all. This may have been due to their inability to persist at higher elevations due to lower ecologically adaptability than apex predators. Indeed only montane specialist large herbivores such as Alpine chamois (*Rupicapra rupicapra*) and Pyrenean chamois (*R. pyrenaica*) regularly live at high elevations and currently are listed as Least Concern on the IUCN Red List having suffered no known large-scale historical declines (Aulagnier *et al.* 2008; Herrero *et al.* 2008). Conversely many large European carnivores live at a range of elevations and have probably been able to prey switch where necessary, especially given the many Holocene introductions of wild and domestic herbivores across Europe (Zeder 2006b; O'Connor and Sykes 2010). Species that were unable to survive at high elevations may therefore have been extirpated earlier and at lower human densities in lowland areas than species that could survive in mountainous areas.

6.5.2 Human population density and large mammal decline

HPD is clearly a major driver of mammalian declines. However, spatial and temporal patterns of decline (figs. 6.2, 6.3) indicate that extinction trajectories may have differed across species. By including information on extinct and extant populations, I was able to go beyond simply identifying HPD as a broad correlate of mammalian extirpations and begin to tease out its variation as a relative driver of decline across specific species through time.

Declines of just over half of all species were significantly related to HPD and these were overwhelmingly the larger-bodied mammals (Table 6.2, fig. 6.4). The 11 smallest species were either extant or showed no relationship with HPD apart from the otter which also had a sample size substantially below the recommended EPV, so that this result may not have been entirely reliable. Conversely, persistence of the eight largest species all showed a significant relationship with HPD, apart from red deer (*Cervus elaphus*). The resilience of red deer to humans could reflect historical management of this species for hunting (Birrell 1992). Critical HPD threshold calculations confirmed that, whilst different species were able to tolerate differential levels of HPD, larger species generally had lower tolerances than smaller species, with the largest not persisting beyond around 13 people per km². These were also predominantly the herbivores: aurochs, European bison, elk, wild horse and wild ass. Interestingly the three carnivore species which are currently the focus of European conservation efforts, bear, lynx and wolf (*Canis lupus*) (Linnell *et al.* 2008), all showed the highest tolerances to HPD, substantially higher than for most of Europe's largest mammals, at between around 77 to 87 people per km² (Table 6.2). This is almost definitive evidence for the existence of an extinction filter (Balmford 1996) that has prehistorically and historically removed populations of low-HPD tolerant species from higher HPD regions of Europe, leaving those species that were most resilient, but which are only now at risk as human populations have increased. Figure 6.3 also highlights that the large mammal species that were least tolerant to high HPD were generally extirpated earlier and therefore more likely to have disappeared prior to historical memory.

Although not all species had a significant association with HPD, there was still an overall significant relationship between body mass and the critical HPDs that large mammals were able to tolerate (fig. 6.6), the first time such a relationship has been demonstrated, to my knowledge. Furthermore, by using information on extant populations over time, I was able to confirm that this relationship was consistent across the large mammal assemblage (fig. 6.7).

6.5.3 Ongoing human activity and its impact on large mammal persistence

However, long term data on the relative extirpation and persistence of different species also reveals that, whilst human populations have been a major threat to large mammals throughout the Holocene Epoch, they have not continued to be a necessary determinant of species persistence into the present day. Some species that have previously been extirpated from parts of their historical range currently thrive in areas of even higher HPD (fig. 6.5). Elk for example became extinct in much of central and western Europe during the early and late Medieval (Schmölke and Zachos 2005) but is extant in areas of eastern and northern Europe today (Henttonen *et al.* 2008). Beaver also experienced rapid declines in the recent historical period but is currently extant in much of Europe (Halley and Rossell 2002) and European bison became entirely extinct in the wild but now survives in small areas of Poland, Belarus and Ukraine (Olech 2008).

Such a phenomenon can largely be attributed to the current conservation movement that has particularly emerged over the past half century across Europe and that has implemented interventions in the form of both species-specific and Protected Area (PA) programmes. Thus an intensive genetic and population management project was set up to recover European bison from the few captive individuals left at the beginning of the twentieth century and which now thrive in national parks in Poland and Belarus (Krasinska and Krasinski 2007). Likewise active reintroductions have restored beaver to much of its former habitat across Europe from a low of 1200 individuals across eight fragmented populations, facilitated by both protection of the species itself and ecosystem protection and management (Halley and Rossell 2002). The beaver is also no longer targeted for its castoreum, fur and meat, and levels of concerted persecution have diminished alongside active protection for many species. International conservation law has also facilitated the requirement of European countries to commit to conservation objectives, both at the species and habitat level (Rodgers 2013). Thus wolf and golden jackal for example, protected from persecution, have naturally begun to recolonise former areas of their historical range (Valière *et al.* 2003; Arnold *et al.* 2012). Forms of protection and/or management are also not exclusive to the development of twentieth century conservation, particularly in Europe, where species such as red deer and fallow deer (*Dama dama*) were preserved in hunting parks since the Medieval Period (Birrell 1992; Rollason 2012) and which may have contributed towards their widespread survival over and above Europe's other largest mammals (fig. 6.5).

This suggests that whilst high HPD is a major threat to wildlife populations, its effects can be mitigated by concerted protection in the form of species-specific conservation programmes and the protection of

species' habitats, a conclusion also noted elsewhere (Linnell *et al.* 2001). Indeed, the importance of targeted conservation efforts cannot be overstated. The two largest species that experienced some of the earliest extinctions in Europe were aurochs and European bison, both of which became extinct in the wild due to traits which increased their vulnerability to human pressures but also due to a lack of protection or management. However, most of their extant Asian bovine relatives are currently living in areas where HPDs already exceed those that drove the aurochs and bison to extinction in Europe (fig. 6.8) and these species are highly threatened as a result. The kouprey (*Bos sauveli*) may in fact already be extinct (Timmins *et al.* 2008a) whilst the gaur (*B. gaurus*), wild yak (*B. mutus*) and banteng (*B. javanicus*) are listed as either Vulnerable or Endangered with declining populations (Duckworth *et al.* 2008; Harris and Leslie 2008; Timmins *et al.* 2008b). Historical information on the tolerance of their extinct relatives to human pressure highlights that these Asian species require immediate conservation attention if they are to avoid the same fate on yet another continent undergoing rapid human population growth.

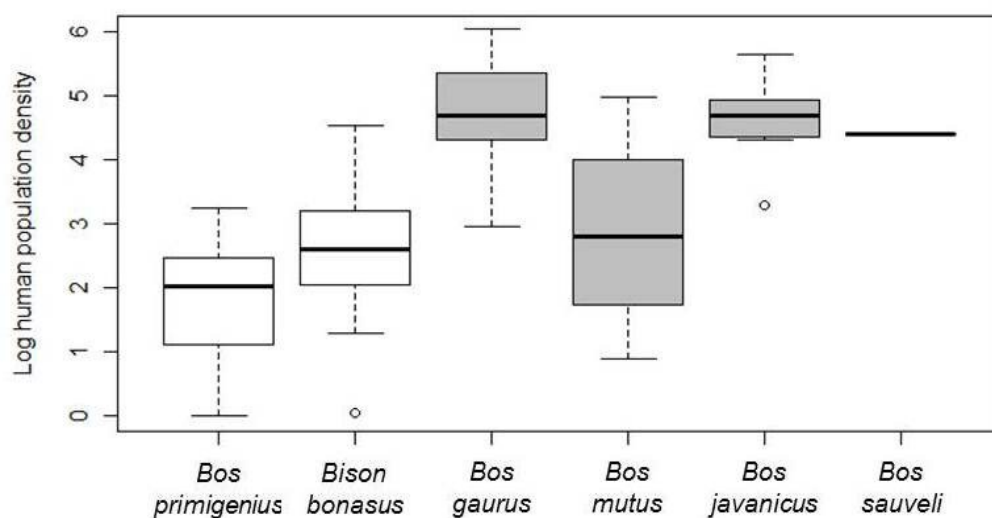


Figure 6.8 Average human population density (HPD) across the extinct ranges of 2 large bovids from Europe (white bars) and across the range of 4 large extant bovids from Asia at AD 2000 (grey bars). HPD data for Asian bovids are taken from country level or, in the case of *Bos mutus*, province level of China. Ranges are taken from IUCN (Duckworth *et al.* 2008; Harris and Leslie 2008; Timmins *et al.* 2008a; Timmins *et al.* 2008b).

6.6. Conclusion

Growing human populations have been a critical driver of the regional loss of European large mammal faunas throughout the Holocene period. However, the negative effects of human activity have not been equally witnessed across the assemblage; those species with a higher body mass were more likely to have experienced regional extirpation and were less tolerant to increasing human population densities. For some species, an extremely low tolerance led to complete regional extirpation in the wild at critical levels of human population early on. However if species were able to

persist in even marginal areas into the recent past, they generally benefitted from protection and/or management thanks to the emerging conservation movement of the late twentieth century. Nevertheless, many of Europe's mammals remain in a critical state with vastly reduced distributions comparative to their historical spread and with little prospect of returning to much of their former range. Therefore information from the past regarding species-specific tolerances to anthropogenic landscapes should remain an important component in the future conservation planning and management of these species.

Chapter 7. Concluding Remarks

7.1 Aims of the thesis

We are arguably in the middle of the Earth's sixth mass extinction (Barnosky *et al.* 2011) uncontroversially driven by human action, and therefore an increased understanding of biodiversity decline is imperative. However, present-day species extinctions are only the latest in a longer sequence of global extinctions that took place throughout the Late Pleistocene and Holocene as a result of (primarily) human activity, and newly discovered but already-extinct species continue to be described (Turvey and Cooper 2009). Macroecological research into patterns of extinction risk that are based on the present-day distribution of biodiversity and biodiversity threat are therefore potentially biased, since this has already been through a major historical extinction filter, resulting in depauperate faunas in many parts of the world. Furthermore, despite increased documentation of past species extinctions we still have limited understanding of the processes that led to their demise. The aim of this thesis was therefore to utilise the extensive but currently under-exploited zooarchaeological record of Europe to reconstruct the patterns (spatial and temporal dynamics) and processes (causative drivers) of mammalian declines in Europe from the Holocene to the present day. By combining information on species that have become extinct as well as species which have survived, it should be possible to identify the principal correlates that have driven species to extinction over time and in particular whether there are indeed common patterns to species decline or whether it has been species-specific. As the first major quantitative study of its kind based on zooarchaeological data, a key aim was also to assess how far information from the past could be combined with data from the present and used to inform conservation science.

7.2 Summary and discussion of main results

Before embarking on analyses based on past species occurrence data it is prudent to acknowledge potential biases associated with different sources of data. The first chapter of the thesis therefore aimed to identify sources of bias across the zooarchaeological dataset. Unsurprisingly, species were not equally abundant; however this would be expected in an ecological dataset, regardless of biases associated with taphonomy. Therefore I compared relative abundances of species from the zooarchaeological assemblage with comparable data from an ecological dataset, in order to detect whether sources of taphonomic bias were influencing which species appeared most frequently in the archaeological record over and above that which would be expected from an ecological assemblage. Herbivore and ecological generalist species were more abundant in the zooarchaeological record than carnivores and ecological specialists, although body mass may also have been supporting this underlying trend. Compared with an ecological dataset of body mass-abundance distributions, the zooarchaeological data demonstrated a potential bias in favour of larger species. Unfortunately, the

species for which I had zooarchaeological data did not cover a wide range of body mass distributions and therefore this result was not conclusive. However, size may not be a necessary determinant of representation in bone deposits as there are fairly comprehensive terrestrial Holocene records for birds (Turvey and Blackburn 2011), reptiles (Case *et al.* 1992) and amphibians (Rocek and Sandera 2008). Indeed, a more detailed analysis of the data suggested that body mass may have influenced carnivore abundance in the zooarchaeological record but that ecological (diet) specialisation may have determined herbivore abundance. Therefore, the effects of taphonomy may not even be equally reflected across assemblages or species. This chapter therefore cautioned against using zooarchaeological datasets at face value, particularly when using them for the purposes of wide-scale macroecological analyses, as the zooarchaeological record may not faithfully reflect underlying communities.

A principal objective of the thesis was to examine different processes of species decline, including range fragmentation, range shifts and range contraction. I chose to analyse the decline of European wild ass (*Equus hydruntinus*) separately from other large mammal species, as available information on the species indicated that it was widespread during the Late Pleistocene and therefore principally adapted to dry, open environments (Burke *et al.* 2003; Antunes 2006) rather than the predominant temperate forests of Holocene Europe. Furthermore, its low abundance in the zooarchaeological record and early extinction indicated that it may have experienced a different extinction trajectory to other species. Indeed, available evidence indicated that, rather than expanding its range during the Early Holocene, as with the other large mammal fauna, it retreated and fragmented into isolated populations in southern Europe. Thus, it was better considered as comprising part of the assemblage of Pleistocene megafauna to undergo temporally staggered, protracted declines across the Pleistocene-Holocene boundary (Stuart and Lister 2007), rather than with the temperate-adapted large mammal faunas that experienced declines from the Late Holocene onwards. The extinction of the European wild ass appeared to be driven by vegetation changes caused by wide-scale climate change at the end of the Pleistocene. However, rather than becoming immediately extinct, it survived in continued areas of open landscape across southern Europe, before its small and isolated populations probably succumbed to human hunting. This chapter made an important contribution to our understanding of Eurasian Late Pleistocene extinctions, spatial processes of species' range decline and also the, currently under-studied, characteristics of interglacial refugia (Bennett and Provan 2008).

Up until now, the majority of research into Holocene mammalian range shifts consisted of comparisons of historical and present day range maps. However, this approach failed to detect diverse trajectories of decline across different species and therefore uncover their relative vulnerability to Holocene human impacts, in particular for species which became extinct during this time. In Chapter 5 I therefore aimed to reconstruct past species ranges from the Mesolithic to the Late Medieval in order to analyse spatial and temporal patterns of Holocene mammalian range shifts. Mindful of results from Chapter 3, I was wary of the potential pitfalls associated with reconstructing

past species ranges based on raw zooarchaeological data due to biases related to differing abundance of species. Initial scrutiny of the data indeed indicated that range measurements (EOO) were positively related to the number of zooarchaeological records making up the range. Due to the fact that sampling varied taxonomically, spatially and temporally (Chapter 2, Chapter 3), I was therefore unable to detect genuine declines in range from changes due to sample size. However, resampling was an effective method to overcome this source of data bias and demonstrated that simple measures can be taken to deal with the analysis of potentially biased information such as fossil and zooarchaeological data. This chapter also highlighted that sources of bias are rarely considered in many spatial studies based on opportunistically collected historical, zooarchaeological or fossil data. Whilst information on past faunal occurrences can be used in wider macroecology, where sampling is necessarily uneven, raw data cannot be used uncritically.

As a result of some data deficiency I was also unable to reliably reconstruct past distributions for six species (Iberian lynx, European mink, wolverine, lion, leopard and reindeer). Although zooarchaeological data were not available for all focal species (Chapter 2) it is also likely that other species such as tiger, saiga and arctic fox would have been too rare in the zooarchaeological record to include in the analysis. This has important implications for the use of species occurrence data from bone assemblages for species that are likely to have been ecologically rare, or rare due to human agency.

However, this does not necessarily mean that such data should be discarded, rather that it should perhaps be used alongside other types of information. Few studies have combined different data sources to analyse changes in biodiversity, partly due to different biases associated with each (e.g. Boakes *et al.* 2010). Yet combining the zooarchaeological record with more contemporary data, such as historical and ecological, could aid long-term, through-time analyses of extinction and survival across species. I used all three types of data in Chapter 6 to reconstruct regional last-occurrences of different European large mammals throughout the entire Holocene Epoch up to the present day. Using long-term information on the timing of regional losses of species allowed me to conduct a detailed analysis of tolerances of species to human population density (HPD) over time that influenced their survival or extirpation. I was also able to analyse the long-term correlates of decline rather than analysing correlates of extinction risk based on the current day survivors, as with the majority of studies to-date. I confirmed that not only did a large body mass and high HPD negatively influence a species' ability to persist, but also that these factors were linked, with large species becoming extinct at lower HPDs and vice versa.

Overall I found that mammalian declines in Holocene Europe were species-specific in their timings, with significant declines starting from the Iron Age to the Late Medieval and many species not declining at all by this time (Chapter 5). Drawing on all data from the Early Holocene to AD 2000 also confirmed different timings of regional extirpations across all species (Chapter 6). However, the individualistic nature of species declines appeared to be underpinned and driven by broad ecological

traits. For example trophic level was associated with species extirpations, with herbivores in general declining prior to carnivores (Chapter 5) and body mass also influenced survival, with larger species declining before smaller species (Chapter 6). However, it is likely that trophic level and body mass are linked, and may also be related to other underlying ecological traits such as reproductive output.

This has important implications for the use of long-term data in understanding extinction risk, as biological traits that predispose extinction can be filtered out by the use of short-term data. One of the major arguments emerging from this thesis is therefore to substantially extend our temporal baselines for conservation in areas where there is a long history of human impact. Due to the persistent nature of human alteration of ecosystems throughout the Holocene, even historical (e.g. centennial) baselines may prove inadequate, since humans have been removing and introducing species around many continents long before historical memory. The choice of baseline to use is ultimately that of conservation practitioners, particularly as the exact point in time that is chosen to represent a 'target' for conservation management can be debated. However, decisions should be made in full awareness of past biodiversity and ecosystem changes, rather than on unknowingly biased information.

Despite the temporally species-specific nature of most large mammal declines there was some congruency to spatial aspects of decline related to humans. For example, most species showed general trends of extirpation from areas of high human density, with ranges in general shifting towards northern and eastern Europe, or towards areas of high altitude, areas which retain most large of Europe's mammal fauna today (Chapters 5 and 6). Conversely, European wild ass displayed a unique trajectory to extinction (Chapter 4), with its distribution highly fragmented by the Early Holocene rather than experiencing wholesale contraction. However as aforementioned, this was principally linked to its status as a probable refugee species in contrast to Europe's other large mammals, and was responding primarily to climate-driven vegetation change rather than human impact.

The long-term perspective that zooarchaeological data offers on the vulnerability of different species could inform mammal conservation prioritisation on other continents experiencing rapid human population growth. For example, this thesis demonstrates that equids and bovids have fared the worst out of all European large mammals, with all four species (wild horse, wild ass, aurochs and bison) becoming extinct in the wild. Whilst only the bison receives any conservation attention today, the importance of these species in the landscape of Europe is evident from the widespread use of their bred-back ecological 'substitutes', including Konik ponies and Heck cattle for conservation management (Buckland *et al.* 2005). Long-term data are also informative for rewilding efforts here in Europe. For example, the results suggest that carnivore species have historically been more resilient to human impacts, are more ecologically adaptable and can survive in even degraded landscapes, despite their heightened threat status today. However, in general, those areas where they persist should not be identified as optimal habitat, particularly upland areas. There is no evidence that this is either suitable or optimal habitat, since they have been widespread over all lowland areas of Europe, but they are currently areas of refuge from humans. Conversely, it appears that large tracts of lowland

habitat are required for the conservation of most large herbivores, principally why it is only in areas of northern and eastern Europe that bison and elk survive. Furthermore, the evidence indicates that large herbivores are less tolerant to high human population densities than carnivores unless they are heavily managed, which may influence the locations for suitable reintroductions.

Finally, in compiling this thesis, I was struck by Europe's past large mammal diversity. A number of surprising species (e.g. tiger, lion, leopard, saiga) spread well into south-eastern Europe before being slowly pushed back, and during the Early-Mid Holocene much of Europe would have been teeming with wild populations of over 30 large mammal species, without including those that were range restricted. It was a sobering reminder of the biodiversity potential of the continent under low human pressures. Conservation has been successful in returning some species from the brink of extinction, such as bison and Alpine ibex, but at the last comprehensive assessment only 8% of mammal species had increasing populations and many remain threatened (Temple and Terry 2007). The ever-present danger of 'shifting baseline syndrome' risks lulling us into a false sense of complacency over the status of mammal conservation in Europe, and it is easy to dismiss 'historical' extinctions as being the responsibility of past generations, something that we are powerless to do anything about now. Yet long-term data crucially reveal the gradual loss of populations over time that is in fact a continuum leading from the past up to the present day, and which we can step in at any time to halt.

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Appendix 1. A review of the European wild horse *Equus ferus*

Introduction

The sole native Holocene European caballoid, *Equus ferus ferus* Boddaert, 1785, became extinct in the wild in 1879, and in captivity fewer than one hundred years ago, in 1918 (Heptner 1934). As one of Europe's few charismatic megafaunal species to have survived beyond the Pleistocene to recent times, there has been surprisingly little research into its ecology, range collapse and eventual extinction.

Equid species are now recognised as forming part of a highly threatened family. The European wild horse is not the only equid to have become extinct: the European wild ass (*E. hydruntinus*) probably became extinct around the Iron Age (Mashkour *et al.* 1999; see also Chapter 4); the quagga, an extinct subspecies of plains zebra (*E. quagga quagga*) became extinct in 1883, following the death of the last remaining individual in Amsterdam Zoo (Hack *et al.* 2008); and a subspecies of Asiatic wild ass, the Syrian wild ass (*E. hemionus hemippus*), became extinct in 1927 (Moehlman 2002; Moehlman *et al.* 2008). Of the seven extant species of wild equid, four are reported as threatened and another, the Przewalski's horse, *E. f. przewalskii*, became extinct in the wild following the last confirmed sighting in 1969 (Moehlman 2002), although it is now classified as Endangered following reintroduction in Mongolia (Boyd and King 2011). Equids are acknowledged to be at risk of extinction and as high priorities for conservation attention and research (Moehlman 2002; Isaac *et al.* 2007).

The European wild horse was among several species of large mammal to experience severe range contraction throughout the Holocene in Europe. Subfossil records demonstrate that species such as aurochs (*Bos primigenius*), European bison (*Bison bonasus*), elk (*Alces alces*), wolf (*Canis lupus*), bear (*Ursos arctos*) and lynx (*Lynx lynx*) were once widespread across the European landscape (Benecke 2005; Schmölke and Zachos 2005; Sommer and Benecke 2005a, b, 2006), in comparison to their present-day ranges (e.g. Mitchell-Jones *et al.* 1999). Progressive loss of populations of large mammal species over the past few thousand years has left only remnant populations of the continent's once diverse megafauna. Chapter 4 reconstructed the Holocene ranges of Europe's large mammal fauna through time using the zooarchaeological record, and modeled their spatial and temporal decline.

However, it was not possible to subject the wild horse to the same analysis for a number of methodological reasons. The Holocene record of the wild horse is fairly well documented up to around the Neolithic; however, beyond this point the domestic horse begins to appear in the Holocene record and zooarchaeologists are in general not happy assigning incontrovertible wild status to specimens (Sommer *et al.* 2011). This is partly because differentiation between wild and domestic forms of horse is extremely difficult (Olsen 2006), as there are few morphological markers, but also because the complex nature of the domestication process (Larson and Burger 2013) means that it was probably not a straightforward case of replacement of wild by domestic forms. Rather, there may have been intermediary forms of wild, domestic and feral hybrids. Furthermore, domestication was a

revolutionary event in the development of human-animal relations and therefore is a topic of intense interest for zooarchaeologists (Zeder 2006; Zeder *et al.* 2006). As a result, most research is focused on the archaeological implications of wild horse decline for timings and origins of domestication events and on the nature of the domestication process, rather than on the fate of the wild horse itself.

However, a better understanding of the history and decline of the wild horse could have implications for both archaeological and zoological disciplines. It would improve archaeological understanding of humans' complex relationship with horses over time, for example, by aiding investigations into domestication processes and timings. It could also aid conservation science research, a central focus of which is to develop an increased understanding of the ecology of species decline and extinction. More broadly, it would also present an opportunity to explore the potential application of Quaternary science to other fields of research and to provide useful interdisciplinary links.

The aim of this review is to collate and summarise the existing literature on the European wild horse, identify research gaps and explore ways to overcome some of the inherent difficulties and limitations into understanding the decline of the wild horse in Europe.

Taxonomy; morphometrics; phylogeography

There has been some confusion over the taxonomy of the wild horse that has yet to be fully resolved. This partly originates from the unknown distribution of the wild horse in the later Holocene which has created uncertainty over the relation of earlier Holocene animals to historically described specimens, usually referred to as 'tarpan'. Unfortunately, the only osteological remains of tarpan are one complete skeleton (St. Petersburg: ZIN 521) and one isolated skull without a mandible (Moscow: MGU 94 535) (Eisenmann 1996). As early Holocene finds also tend to be highly fragmented, there is little scope for morphological comparison of specimens (Olsen 2006).

The first authentic account of a wild horse in Europe is considered to be that of that of the traveller and naturalist Gmelin in 1769 near Voronezh in south-western Russia, of which Zeuner (1963) provided a translation. The same expedition produced the only known drawing of a wild horse from a living example, by Borisov (Antonius 1937) (fig. 1). Boddaert (1785) then described a species that matched Gmelin's account and named it *E. ferus*. However, unaware of Boddaert's (1785) description of the wild horse as *E. ferus*, Antonius (1912) then named the wild horse of Gmelin's description as *E. gmelini*. As the earliest historical designation, the correct name for the wild horse was confirmed by the International Commission on Zoological Nomenclature (ICZN) as *E. ferus* Boddaert, rather than *E. gmelini* Antonius which represents a junior objective synonym (Groves 1994; Gentry *et al.* 2003). The wild horse has also been named by various others on the basis of historical sightings and descriptions (see Wilson and Reeder 2005) but they all postdate *E. ferus* Boddaert. 'Tarpan' is used as the common name for the European/Russian wild horse, as this was the name given to wild horses by Tatars and Cossacks to distinguish them from feral horses (Groves 1994). This species was also

therefore described as *E. tarpan* Pidoplichko (1951), now considered a *nomen nudum* (Grubb 2005 in Wilson and Reeder 2005).

However, as the domestic horse was first described as *E. caballus* by Linnaeus, 1758, before the first description of wild horses, this was the name given to the species by Grubb (2005). Groves (1971) and Corbet (1978) suggested that *ferus* replace *caballus*, as they objected to the use of a species name based on a domestic form. Gentry *et al.* (1996) then proposed that that the majority usage name be adopted, but Grubb (2005) argued that it had not been demonstrated that most authors used *E. ferus* rather than *E. caballus* or *E. c. ferus*. The ICZN ruled in favour of recognising the name *E. ferus*, but did not stipulate what name was to be used by those who considered *caballus* and *ferus* to be conspecific (Gentry *et al.* 2003). Grubb (2005) argued that since there had not been sufficient research into the systematics of the wild horse and as its status was still disputed, that within Wilson and Reeder (2005) *ferus* was treated as a subspecies of *E. caballus*.

Groves (1986; 1994) has provided a taxonomic review of the wild horse. The recognition of distinct subspecies has also been considered, based on differing historical descriptions of wild horses, particularly with regards to colouration. Groves (1986) for example considered the possibility that, based on von den Brincken's (1826) description of *E. sylvestris*, there was a form of forest tarpan that differed slightly from the steppe tarpan. However this view has not been widely upheld or substantiated.

The relationship between the tarpan and Przewalski's horse has also not been clarified. They are generally considered subspecies, *E. f. ferus* and *E. f. przewalskii*, which Groves (1994) for example recognised. Heptner (1955, in Groves 1994) argued that there was a zone of intergradation between the two subspecies on the steppes east of the Volga with the two generally distinguished by colour, tarpan being greyer and Przewalski's horse more reddish. Forsten (1988) measured two known tarpan skulls and found the measurements to fall mostly within the size range of Przewalski's horse. However, due to lack of specimens, the metric variation for historical tarpan is unknown. Grubb (2005) did not recognize Przewalski's horse as either a distinct species or subspecies. Przewalski's horse is therefore still variously designated by different authors as *E. przewalskii* and *E. f. przewalskii*, with no published consensus.

Morphometric analysis of Late Quaternary equids has also clouded the picture somewhat. Early research, based on significant size differentiation among horse specimens, suggested that there were several lineages at the end of the Pleistocene, with only the smaller form of caballoid horse surviving into the Holocene (Forsten 1991). However, aDNA analysis indicated that all Late Pleistocene caballine horses from Western Europe to eastern Beringia, including domestic species, were a single Holarctic species (Weinstock *et al.* 2005). Further morphometric (Bignon *et al.* 2004; Anthony 2009) and genetic (Orlando *et al.* 2009; Geigl and Grange 2012) evidence has confirmed high levels of intraspecific variation within equid species and Orlando *et al.* (2009) suggested more generally that morphological plasticity among large terrestrial vertebrates over time and space has probably been underestimated.

It should also be mentioned that the range of the wild horse overlapped with another small-bodied European equid during the Holocene, the European wild ass (*E. hydruntinus*), which became extinct, probably during the Iron Age (Mashkour *et al.* 1999; see also Chapter 4). The Holocene range of *E. hydruntinus* was more southerly than that of *E. ferus*, its northernmost find being in the Czech Republic (Kysely 2005). However, again, little is currently known of its ecology and extinction trajectory (although see Chapter 4) and there has been only one study into the ecological relationship between the two species (Uerpmann 2005); there is therefore much potential for further research.

Distribution of the European wild horse: current evidence

The wild horse was one of few large mammal species that survived the postglacial warming to persist in Europe beyond the end-Pleistocene. Subfossil records attest to its maximum distribution during the last glaciation from Portugal all the way over ice-free parts of Europe to Asia, across the Bering land bridge and into Alaska, with its maximum southward range in southern Jordan and the central Zagros mountains of Iran (Uerpmann 1987; 1995). In the Early-Mid Holocene it persisted in western, central and eastern Europe (Robert Sommer, Christian-Albrechts-Universität zu Kiel, personal communication, 2010; Sommer *et al.* 2011; fig. 2). However, beyond immediately postglacial fossil remains, there is a lack of evidence for *E. ferus* persisting in Scandinavia, the UK, Italy and the Balkans (Benecke 2006).

The postglacial range did extend across the steppe region from Russia to Central Asia, although its distribution in this area has not been well traced (Heptner *et al.* 1988). At the eastern end of this range, the wild horse is described as Przewalski's horse (although it became extinct in the wild in 1969). Its postglacial range also included the Caucasus (Vereshchagin 1959) and Anatolia (Uerpmann 1987), although evidence for its presence in the latter region is somewhat more contested. It had been thought until recently that the wild horse did not survive the post-Pleistocene here, and only reappeared in domesticated form from the Neolithic onwards (e.g. Bökönyi 1991). However, Martin and Russell (2006) have more recently surveyed horse remains from Anatolian Neolithic and Chalcolithic sites (acknowledged to be few) and argued that the *E. ferus* finds that they examined from the Neolithic site of Çatalhöyük, in addition to early Neolithic finds at Aşıklı Höyük (Vigne *et al.* 1999), attested to its early Holocene existence on the Konya Plain, albeit in probably small numbers. However, all Holocene wild horse records in this region only dated from the postglacial up to the Neolithic or Mid-Holocene.

The only other sources of information are historical accounts that originated from the eighteenth and nineteenth century, as well as a few sparse Roman and Greek accounts of wild horses (see Levine 2005a for a summary of some of the main historical accounts). Its historical range, principally based on sightings from travelers and naturalists (Heptner *et al.* 1988), indicated a severely reduced distribution in comparison to mid-Holocene distribution patterns (fig. 2). It must of course be taken into consideration that many of the final accounts of wild horse were describing feral domestic horses or

even feral hybrids, rather than purely wild or domestic animals (Pavel Kosintsev, Institute of Plant and Animal Ecology, RAS, personal communication, March 2013) and there are several accounts of aggressive wild stallions taking over feral or domestic harems, producing hybrids (Gmelin, translated in Zeuner 1963; Mohr 1972; Heptner *et al.* 1988). However, Groves (1986) argued that the majority were wild on the basis that feral or domestic horses would not have been as able to compete with wild forms that had undergone selection for local conditions over some millennia. Heptner *et al.* (1988) also argued that interbreeding or mixing between domestic and wild species probably only occurred in the last fifty to one hundred years, when populations were already decreasing. However, in reality the degree of admixture or interaction prior to historical accounts is not known. The last free-living wild horse was documented in the wild in 1879 on the steppes of the Cherson region in Ukraine, and the last living purported wild horse was kept in captivity between 1914 and 1918 on an estate near Dubrowka in the Poltava region of Ukraine (Heptner 1934).

Between the Mid-Holocene and 1879 we have little knowledge of what happened to this species, in terms of its range decline or extinction drivers, other than recorded direct hunting in the recent historical period. Sommer *et al.* (2011) used radiocarbon dated records of Holocene wild horse to argue that it declined in the Early-Mid Holocene due to postglacial forest growth, but that it markedly increased around the Mid-Holocene, probably due to landscape opening by Neolithic peoples. Holocene environmental change has also been variously cited as leading to the adaptation of a further subspecies of *E. ferus*, that of *E. f. silvestris* (von Brincken 1826), which it is thought to have inhabited the forests of central Europe, whilst *E. f. ferus* inhabited the more open steppe environments of western Asia (Groves 1986). However this view has not been widely accepted.

The fact that wild horses were already rare at the beginning of modern zoological research some two hundred years ago (Uerpmann 1995) has limited understanding of wild equid ecology, and only basic information on wild populations was documented in historical accounts, usually anecdotally, before its extinction in the early twentieth century. It is therefore difficult to infer the key intrinsic or extrinsic drivers of population decline and eventual extinction. However, current (albeit limited) research into the ecology of extant equids suggests that several traits are shared between all species. Allometrically at least, equid species are more similar to each other than species within other ungulate families such as Cervidae or Bovidae, with body mass ranging from 100-450kg (Saltz and Moehlman 2002). Under non-extreme environmental conditions, equid populations exhibit a rapid growth rate. Their ability to survive on low quality forage suggests that poor habitat conditions might have minimal impact on survival, making them relatively insensitive to local environmental changes in forage quality due to seasonal change. However, Sommer *et al.*'s (2011) study suggested that wild horse might be sensitive to more rapid and widespread environmental change such as the relatively rapid reforestation that occurred at the beginning of the Holocene. Due to a lack of stable data, it is unclear what the main population controls were, but they could have been predominantly stochastic or mass mortality events, such as disease or drought. Heptner *et al.* (1988) for example noted that during excessively cold winters, wild horses in Russia were often documented as perishing en masse,

though populations would recover well when they were abundant. Most extant equid populations are declining due to human activity (Saltz and Moehلمان 2002).

Interestingly the historical distribution of wild horse indicates an ultimate overall collapse in range from west to east (fig. 2), a pattern that was similar to the reconstructed range shifts of other large herbivores during the Holocene such as elk (*Alces alces*), aurochs (*Bos primigenius*) and bison (*Bison bonasus*). These species were also relatively widespread across Europe in the early-mid Holocene but their final areas of distribution were limited to eastern Europe, linked to lower human population densities in this region (see Chapters 5 and 6). Therefore whilst the wild horse was able to survive and adapt to postglacial climate change, and even some subsequent habitat alteration, the species was ultimately unable to cope with the effects of persistent and increasing levels of high human population pressure.

Methodological issues with reconstruction of the history of *E. ferus*

Genetically, the wild horse partially survives in its domestic counterpart, and it is on this anthropogenic process that the majority of Holocene equid research has been focused. Horse domestication is a topic of intense research within the zooarchaeological community, yet the wild horse is the subject of interest only in so far as it holds the clues as to the origin and timing of domestication events. There is very little known about its subsequent fate beyond its role as progenitor to domestic horses and the processes that led to its final disappearance.

Beyond the Neolithic, the appearance of domestic forms limits the ability to infer the presence of wild horse or not in a region. Some of the earliest evidence for domestication of the horse is from the Eurasian steppe, dated to around 6000 years ago (Outram *et al.* 2009), from where it spread to eastern Europe and the Caucasus, finally reaching southern and western Europe in the Bronze Age (Bokonyi 1987; Benecke 2006; Warmuth *et al.* 2012), although the specific nature of this process is still widely debated (e.g. Levine 1999; Vila *et al.* 2001; Levine 2005b; Olsen 2006; Kavar and Dovc 2008). Morphologically there is little to differentiate wild and domestic forms of horse from archaeological material. Morphological markers of other domestic species tend to include change in cranial shape, reduced tooth size, body size reduction and shape change in horns (e.g. Zeder 2006). However, stallions, unlike males of many other mammal species, do not display obvious secondary sexual characteristics that might be modified through the process of domestication. Furthermore, given uncertainty about the size of the wild horse and the probable variation in wild populations, size is essentially useless as a marker of initial horse domestication (Olsen 2006).

Zooarchaeologists are therefore reluctant to assign 'wild' status to horse specimens that postdate domestication, resulting in few, if any, wild horse remains reliably dated to beyond the Neolithic/Bronze Age. Many remains beyond this period are speculatively identified as domestic simply through context, i.e. being found with other domestic species (Sandra Olsen, personal communication 2009), which can result in very circular inferences. This is of course not applicable to

countries where there is no record of wild horse populations at all, for example in Italy, where it may then be reasonable to infer that the first appearance of horses represented domestic forms.

It is also possible that there was a shifting gradient from wild to domestic horses perhaps not experienced in other species that makes it too simplistic to assign wild and domestic very easily. Levine (2005b) suggested that wild foals could have been captured and tamed, and even ridden, before eventually being slaughtered for their meat. Feral individuals or herds probably also existed alongside wild and domestic forms; indeed feral herds of domestic horses continue to exist in Europe, for example, in the Camargue in France and in the New Forest and Exmoor in Britain, which are thought to be of relatively ancient origin due to their hardy natures and primitive features (Clutton-Brock 1992). Whether these formed the basis for later historical accounts of 'wild' horses cannot be confirmed, although descriptions of very primitive characteristics, e.g. stiff manes, may be a better indicator of wild forms over feral.

Moving beyond the impasse

An improved ability to identify wild horses in the subfossil record could benefit several areas of research. If it can be shown where and when populations of wild horses became extinct across Europe and western Asia, then its reappearance can more easily be ascribed to those of domesticates (Olsen 2006). A better understanding of the ecology of the European wild horse, as well as the patterns and drivers of its decline, would also be of interest to zoologists and ecologists. This in turn could contribute towards research by conservation biologists into extant equid ecology and the major threats that face their survival.

However, zooarchaeological assignments of 'wild' or 'domestic' in horses should be treated critically. On archaeological sites where there are large amounts of zooarchaeological material, an in-depth analysis may not have been carried out, particularly where the focus of the excavation was not specifically on equids. Controversial designations should arguably be revisited and reanalysed. In general however, lack of time and resources prevent this from being an option.

Some detailed analyses have taken place as examples of how different strands of archaeological evidence can be combined to help clarify such debates. Olsen's work on the Copper Age (3600-2300 BC) site of Botai in Kazakhstan, for example, has been at the centre of a debate over whether the equids present in the archaeological record are wild or represent the earliest known evidence for domestication of horses (Olsen 2003; 2006). Whilst fully acknowledging the morphological difficulties, Olsen nonetheless presented an analysis of other types of evidence or 'markers' of domestication; these included areas such as palaeopathology, population structure analysis and palaeoecology. Whilst none of these would be taken as robust evidence in isolation, the combination of potential factors in context may form a clearer or more plausible picture of either wild or domestic forms being present on any given site.

Levine (1999) also offered a critique of markers of domestication, and presented ethological evidence to highlight the complex potential nature of horse-human relationships. She critiqued the drive to search for the 'earliest date' of horse domestication which she argued makes it easier to use inadequate criteria for the determination of domestication and requires little to be said about the actual relationship between animals and people.

More recent publications have opened up new forms of analysis of wild versus domestic horse. Outram *et al.* (2010) carried out metrical analysis of horse metacarpals, with domestic horses generally exhibiting more slender limb bones than wild horses. Evidence of harnessing and riding was discerned from tooth analysis, using a macroscopic method to quantify the degree of biting damage. Finally, archaeological evidence for horse fat residues in pottery was distinguished, indicating processing of mare's milk and the use of horses for secondary products. Ludwig *et al.* (2009) analysed DNA sequence polymorphisms responsible for coat colour, where an identified rapid increase in the number of coat colours from the fifth millennium BC onwards was taken as evidence for domestication, indicative of selective breeding.

Despite the argument over whether the final wild horses interbred with domestic forms, it is generally accepted that the wild horse survived in parts of Europe until around one hundred years ago, yet we have almost no information on its history up to this point from the Mid-Holocene. It is necessary to abandon circular and assumptive reasoning on the part of zooarchaeologists when faced with equid remains in faunal assemblages. Human relationships with horses have arguably been more complex than with any other animal species, wild or domestic, therefore requiring a more nuanced approach to interpretation of the archaeological record.

In order to fully reconstruct the temporal and spatial dynamics of the decline of the wild horse, as well as its causative drivers, it would also be beneficial to draw together evidence of wild horse across its former range, from Europe across Russia and central Asia to China (e.g. MacPhee *et al.* 2002; Wen 2009; Pavel Kosintsev, Institute of Plant and Animal Ecology, RAS, personal communication, March 2013). Furthermore, as the appearance of the domestic horse was non-congruous across its wild range (for example the domestic horse appeared later in China than in western Europe (Yuan and Flad 2006)), there may be areas with a longer temporal framework in which to interpret dynamics of wild horse populations before the appearance of domestic forms.

The future of an extinct mammal: zooarchaeological and conservation implications

Untangling the Holocene history of the wild horse and studying the causes of its decline and extinction are among the more challenging tasks for zooarchaeologists, ecologists and conservation scientists. That so little is understood about a recent historical extinction of one of Europe's charismatic megafauna is surprising. Due to the interest in horse domestication and its impact on human society, the fate of its wild progenitor has been somewhat neglected. As outlined above, a lack of interest has been compounded by serious methodological challenges.

In summary:

1. There is a need to strive for greater consistency in methodologies of excavation, analysis and interpretation of equid remains in zooarchaeological assemblages. Zooarchaeologists need to provide a more rigorous critique of 'wild' and 'domestic' designations to horse remains, potentially revisiting controversial and/or under-studied assemblages, using the full context of a site rather than isolated markers.
2. More research in general is needed into the period of prehistory between domestication and historical records of wild horses.
3. A greater overlap is needed between zoologists, zooarchaeologists and ethologists to begin to answer relevant questions to each discipline. The potential outcomes of this research should be recognised as inter-disciplinary and as contributing to a number of fields such as archaeology, zoology and conservation.

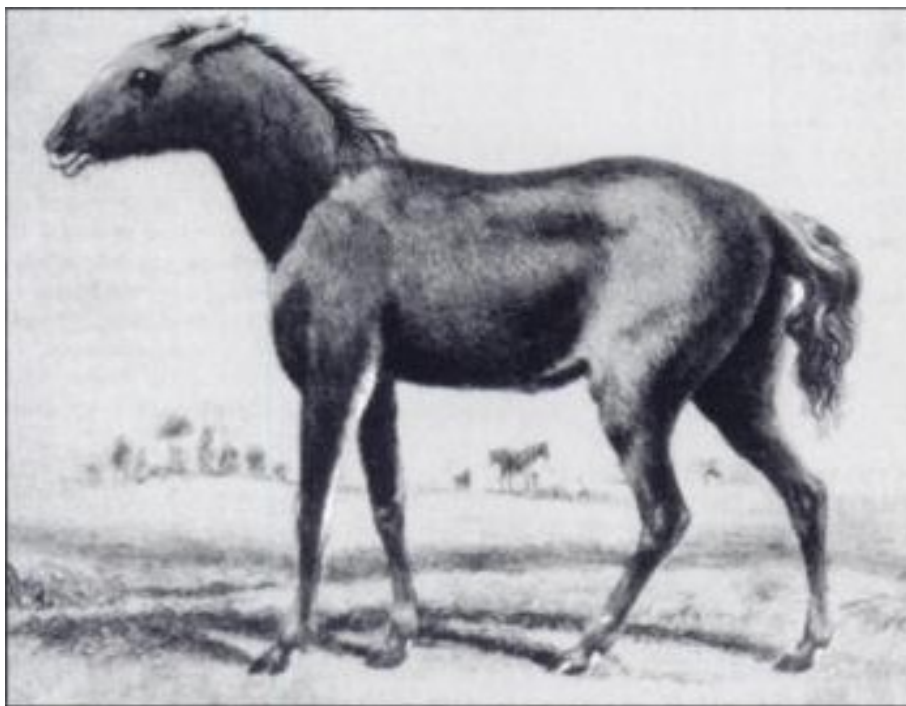


Figure 1 The only known illustration based on a live tarpan, a five-month old foal (Borisov, 1841).

(a)



(b)



(c)

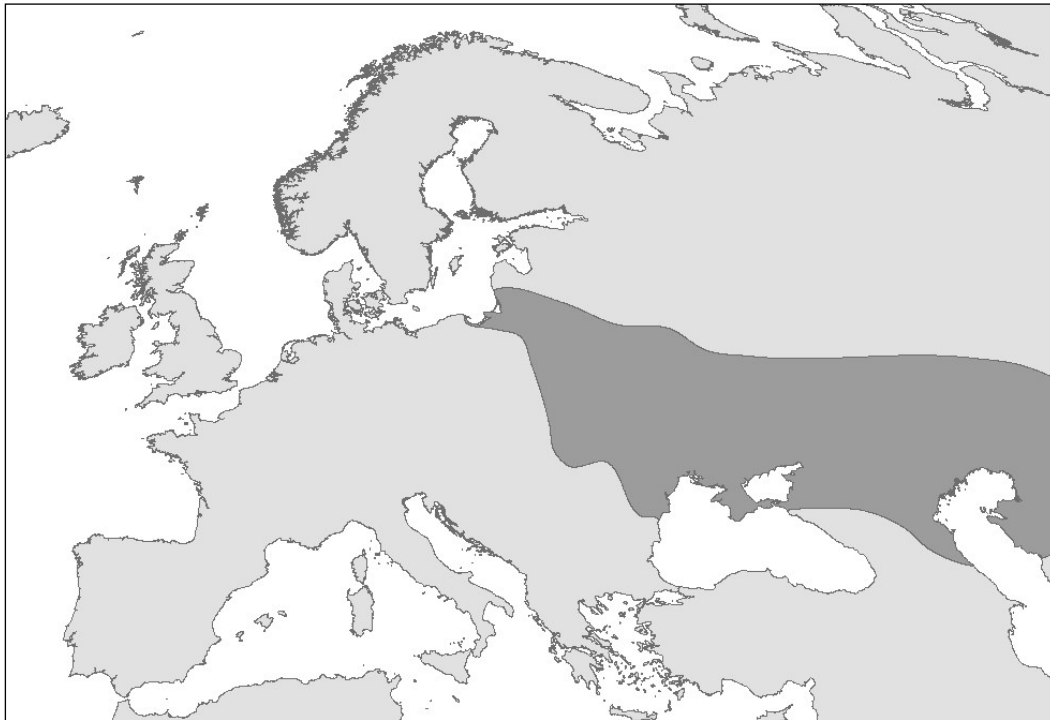


Figure 2 Evidence for the Holocene distribution of the wild horse during the: a) Mesolithic (10500 – 5500 BC) and b) Neolithic (5500 – 3000 BC); c) historical distribution of tarpan according to Heptner *et al.* (1988).

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Appendix 3. Sources of dating for the Holocene zooarchaeological database

Approximate dates of European cultures

Culture	Date	Reference
Ahrensburg	10800-10000 BP	Blankholm (2008)
Altheimer	3800-3300 BC	Kuhn <i>et al.</i> (2005)
Ancien rhodanien	5400-4800 BC	Voruz (1998)
Andronovo	2300-1000 BC	Lamberg-Karlovsky (2005)
Anglo Saxon	AD 410-1066	World Timelines (2010)
Antiquity (Classical)	753 BC - AD 529	World Timelines (2010)
Antiquity (Late)	c. AD 235-650	World Timelines (2010)
Archaic	c. 800-500 BC	World Timelines (2010)
Argar	A 1800-1600; B 1600-1300 BC	Jordá Cerdá <i>et al.</i> (1986)
Aunjetitz (Unetice)	2300-1600 BC	World Timelines (2010)
Auvernier	2900-2400 BC	Karg and Markle 2002
Auvernier cordé	2700-2450 BC	Cattin <i>et al.</i> 2009
Azilien	12000-9500 BP	Rouch-Zurcher 1999
Azov-Dnepr	4700-4200 BC	Manzura 2005
Baalberg	3800-3350 BC	Probst 1991
Baden	3600/3500 - 2800/2600 cal. BC	Horvath <i>et al.</i> 2008
Baden-Kostolac	3500-2200 BC	Trbojevic Vukicevic <i>et al.</i> 2006
Bajca-Retz	4000-3500 BC	Whittle 1996
Balanovo	3200-2300 BC	Mallory and Adams 1997
Balaton	4000-3500 BC	Whittle 1996
Balkengrab (Timber Grave)	1800-1200 BC	http://archaeology.about.com/od/tterms/g/timbergrave.htm
Banat	5850-5470 cal. BC	Spataro 2006
Bandkeramik	5700/5500-5000 cal. BC	Srauble 2006
Bernburg	3200-2800 BC	Probst 1991
Bodrogkeresztur	3830-3485 cal. BC	Bankoff and Winter 1990
Boian	5300-4600 BC	Whittle 1996
Britzer	3500-3200 BC	Fischer Zujkov 2000
Bug-Dniestr	6300-5900 cal. BC	Kotova 2009
Bukk	5200-4500 BC	Körös Regional Archaeological Project 2007
Carolingian	686-840 AD	World Timelines (2010)
Catacomb Grave (Katakombengrab)	2800-2200 BC	Mallory and Adams 1997
Cernavoda	3700-3000	Whittle 1996
Chamer Gruppe	3030-2780 cal. BC	Ottaway 1999
Chasseen	4000-3400 BC	Gallay 2010
Clairvaux ancien	3400-2450 BC	Gallay 2010
Classical	500-323 BC	World Timelines (2010)
Cluj-Cheile Turzii-Lumea Noua	5000-4800 BC	Sanda 2007
Comb Ware (Kammkeramik)	4200-2000 BC	Mallory and Adams 1997
Corded Ware	2800-2400 BC	Whittle 1996
Cortailod	4100-3400 BC	Whittle 1996
Cotofeni	3500-2500 BCE	Raczky 1995
Coslogeni	1400/1300–1050/1000 BC	Marinova and Atanassova (2006)
Cotogeni	1400/1300–1050/1000 BC	Marinova and Atanassova (2006)
Cris (Lower Danube)	6400-5700 BC	Whittle 1996
Cris (Moldavia and Ukraine)	6400-5500 BC	Whittle 1996
Csöszhalom	4500-4100 BC	Archaeology Data Service UK 2010
Cucuteni	A1-IV 4600-4050; A/B 4100-3800; B 3800-3500	Mantu 1998
Dimini	4800-4500 BC	Greek Thesaurus 2010
Dniepr-Donetz	6500-4750 BP	Whittle 1996
Dudesti	5700-5300 BC	Whittle 1996
Duvensee	8500-6500 cal. BC	Holst 2010
Egolzwil	4300-4000 BC	Mueller Science 2010
Einzelgrab	2800-2300 cal. BC	Holtorf 1998
Ertebolle	6500-5100 BP (C14)	Blankholm 2008

Ertebolle	5300-3900 BC	Whittle 1996
Ertebolle - Ellerbek	5760+/-100	Gob 1990
Facies Großgartach	5000-4500 BC	Schmitz 2004
Fontbouissee	2600-2300 BC	Vander Linden 2006
Furchenstichkeramik	5000-4500 BC	Whittle 1996
Fuzesabony	1950-1650 cal. BC	Sørensen and Rebay-Salisbury 2008
Gava	1350-935 BC	Pare 1996
Geometric	1050-700 BC	Greek Thesaurus 2010
Glina III-Schneckenberg	2600-2000 BC	Machnik 1987
Globular Amphora (Kugelamphora)	3570-2470 cal. BC	Ottaway 1999
Glochenbecher (Bell Beaker culture)	2500-2000 BC	Price <i>et al.</i> 2004
Grebenikov	6439-6404 cal. BC	Kotova 2009
Grubchenkeramisch (Pitted ware culture)	3200-2300 BC	Zvelebil 2004
Gumelnitsa	4600-3700 BC	Whittle 1996
Gyulavarsánd	2150-1400 BC	Duffy 2010
Hallstatt	A & B 1200-700 BC ; C 700- 600 BC ; D 600-475 BC	James 2005
Hamangia	4500-4250 BC	Slavchev 2004
Hatvan	1950-1650 cal. BC	Sørensen and Rebay-Salisbury 2008
Havellandische	3200-2800 BC	Probst 1991
Helladic	Early Helladic I 3300-2900; Early Helladic II 2900-2100; Early Helladic III 2100-1900; Middle Helladic 1900-1600; Late Helladic I 1600-1500; Late Helladic II 1500-1400; Late Helladic III 1400-1060	Budin 2004
Hellenistic	323-146 BC	Encyclopedia Britannica 2010
Herpaly	4500-4100 BC	Archaeology Data Service UK 2010
Horgen	3400-2800 BC	Whittle 1996
Hornstaader	4100-3900 BC	Probst 1991
Horodistea-Foltesti	3000-2500 BC	Sherratt 2005
Hunyadihalom	3600-3400 BC	Donau Archaeologie 2010
Jastorf	600-0 BC	Brandt 2001
Karanovo I-II	6450-5750 BC	Whittle 1996
Karanovo III	5750-5250 BC	Whittle 1996
Karanovo IV	5250-4800 BC	Whittle 1996
Karanovo V-Maritsa	4800-4350 BC	Whittle 1996
Karanovo VI	4350-4000 BC	Whittle 1996
Karanovo VII	3300-2700 BC	Whittle 1996
Kongemose	6000-5200 BC	Kozłowski and Kozłowski 1998
Koros	6400-5500 BC	Whittle 1996
Kosihy-Caka	2200-2000 BC	Milisauskas and Kruk 2002
Kunda	9100-8300 BC	Stančikaitė <i>et al.</i> 2006
La Tene	475-15 BC	James 2005
Lausitzer (Lasutian)	1400-500 BC	Archaeology Online 2010
Lengyel	5000-4000 BC	Whittle 1996
Lepenski Vir	6180-5720 cal. BC	Obelic <i>et al.</i> 1998
Lietzow	5300-3900 BC	Whittle 1996
Linearbandkeramik	5600-4750 BC	Lenneis and Stadler 1995
Litzenkeramik	c. 1500 BC	Neugebauer 1977
Los Millares	c. 3200-2300 BC	Esquivel and Navas 2007
Ludanice	4000-3700 cal. BC	Banffy 2002
Lüscherz	2900-2700 BC	Cattin <i>et al.</i> 2009
Lutengüetle	4250-4000	Schmitz 2004
Mad'arovce	1900-1400 cal. BC	Forenbaher 1993
Maglemose	10000-8000 BP	Blankholm 2008
Magyarad	1500-1300 BC	Zsolt 2003
Merovingian	AD 450-752	Wood 1994
Michelsberger	4000-2800 BC	Whittle 1996
Migration	AD 375-600	Nikolay <i>et al.</i> 2011

(Völkerwanderungszeit)		
Mondsee	3700-3300 BC	Whittle 1996
Monteoru	3000-1600 BC	Motzoi-Chicideanu 2003
Mullerup	6700-6400 BC	Tauber 1972
Munchshofener	4500-3900/3800 BC	Donau Archaeologie 2010
Murzak-Koba	9100-8000 BC	Bonsall 1989
Mycenaean	1600-1000 BC	Smith 1987
Nagyrév	2450-2050 cal. BC	Sørensen and Rebay-Salisbury 2008
Narva	5000-2800 BC	Stančikaitė <i>et al.</i> 2006
Nizhnedonskaya	6050-5250 BC	Kotova 2009
Noua	1600-1100 BC	Motzoi-Chicideanu 2003
Ottomani	2400-1500 BC	Forenbaher 1993
Pare	1350-935 BC	Pare 1996
Pecica	2500-1700 cal. BC	O'Shea 1995
Pfyn-Cortailod	4100-3400 BC	Whittle 1996
Pre-cucuteni	5100-4600 BC	Mantu 1998
Prikazanskaja	1400-800 BC	Chalikov 1980
Protovillanoviano	1100-900 BC	D'Agostino 1966
Przeworsk	200 BC - AD 500	Mallory and Adams 1997
Rachmani	4500-4000 BC	Manning and Bruce 2009
Rivnac	3000-2800 BC	Kysely 2008
Rossen	4400-4100 BC	Whittle 1996
Rubané recent	5200-4700 BC	Whittle 1996
Salcuta	4500-3900 BC	Bankoff and Winter 1990
Sauveterrien	8500-6500 BC	Fedele 1992
Schela Cladovei	7450-6645 cal. BC	Bonsall <i>et al.</i> 2000
Schnurkeramik (Cord Ware)	2800-2200 BC	Furholt 2003
Schonfelder Gruppe	2300-1800 BC	Starling 1983
Schussenrieder	4200-3500 BC	Probst 1991
Scythians	800-400 BC	Encyclopedia Britannica 2010
Seine-Oise-Marne	3400-2900 BC	Naudet and Vidal 2001
Sesklo	5300-4400 BC	Rutter 2010
Shan Koba	9000-8000 cal. BC	Sherratt 2005
Single Grave	2800-2300 cal. BC	Holtorf 1998
Sitagroi III	4500-3600 BC	Whittle 1996
Sitagroi IV	3600-3000 BC	Whittle 1996
Somogyvár-Vinkovci	c. 2500-2000 BC	Savel 2006
Sopot	5480-5070 cal. BC	Obelic <i>et al.</i> 2007
Srednij Stog	5100-4300 BC	Kotova and Makhortykh 2008
Srubnaja	2000-1000 BC	Lamberg-Karlovsky 2005
Starcevo	6500-5500 BC	Whittle 1996
Stichbandkeramik	5000-4500 BC	Whittle 1996
Streitax (Battle Axe)	2800-2200 BC	Furholt 2003
Sursko-Dniepr	6000-5500 cal. BC	Sherratt 2005
Szalkhat	5260-4880 BC	Körös Regional Archaeological Project 2007
Szilmege	5260-4880 BC	Körös Regional Archaeological Project 2007
Talayot	1300-100 BC	Fernandez-Miranda 1997
Tamins-Carosso	3300-2900/2800 cal. BC	Pedrotti 2001
Tardenoisian	8000-5000 BC	Price 1987
Theiss	4800-4400 BC	Whittle 1996
Thessaly I-III; I-IV	3600-1900 BC; 3600-1500 BC	Weinberg 1947
Tiefstichkeramik (Deep Engraving Ceramic)	3500-3000 BC	Beier and Einicke 1994
Tisza	4800-4400 BC	Whittle 1996
Tiszadob, with Bükk and Esztár	5200-4500 BC	Archaeology Data Service UK 2010
Tiszapolgar	4400-3800 BC	Whittle 1996
Trichterbecher	4000-3250 BC	Whittle 1996
Tripolye	A 4800-4500; BI-BII 4500-4000; BII 4000-3800; CI-CII 3800-3500	Mantu 1998
Turdas	5500-5000 BC	Whittle 1996
Urnfield	1300-750 BC	Karavanic 2009

Varna II	4500-4000 BC	Whittle 1996
Vatina	2000-1300 BC	Forenbaher 1993
Vatya	1950-1650 cal. BC	Forenbaher 1993
Verbicioara	2300-1900 BC	Motzoi-Chicideanu 2004
Vinca	5300-4550 cal. BC	Orton 2009
Volosovo	2500-1800 BC	Emei'yanov 2001
Wikingerzeit - Viking Period	AD 800-1066	Milman and Pedersen 2003
Zeliezovce-Gruppe	c. 5000 BC	Vozárik and Vozárik 2010
Zok	2900-2400 BC	Forenbaher 1993

Approximate dates of archaeological periods of Holocene Europe by country

Country	MESOLITHIC		NEOLITHIC		BRONZE AGE		IRON AGE / DARK AGE (SE Europe)		
	Mesolithic (Early)	Mesolithic (Late)	Neolithic	Chalcolithic (Copper Age) / Eneolithic	(Early) Bronze Age	Middle / Late BA	(Early) Iron Age	Late IA	Persian Empire
British Isles	8800 - 4000 BC		4000 - 2200 BC		2200 - 750 BC		750 - 0 BC		
Ireland	7000-5500 BC	5500-4000 BC	4000-2400 BC	2400-2200 BC	2200-1500 BC	1500-1000 BC; 1000-600 BC	600 BC-400 AD		
Northern and East Europe	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Austria	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Belarus	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Czech Republic	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Denmark	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Estonia	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Finland	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Hungary	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Latvia	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Lithuania	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Norway	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Poland	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Russia	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Slovakia	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Slovenia	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Sweden	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
Ukraine	9000 - 5000 BC		5000-2250 BC		2250 - 750 BC		750 - 450 BC	450 BC-0 BC	
North West Europe	9000 - 5000 BC		5000-3200 BC		3200-750 BC		750 - 450 BC	450-50 BC	
Belgium	9000 - 5000 BC		5000-3200 BC		3200-750 BC		750 - 450 BC	450-50 BC	
France	9000 - 5000 BC		5000-3200 BC		3200-750 BC		750 - 450 BC	450-50 BC	
Germany	9000 - 5000 BC		5000-3200 BC		3200-750 BC		750 - 450 BC	450-50 BC	
Luxembourg	9000 - 5000 BC		5000-3200 BC		3200-750 BC		750 - 450 BC	450-50 BC	
Netherlands	9000 - 5000 BC		5000-3200 BC		3200-750 BC		750 - 450 BC	450-50 BC	
Switzerland	9000 - 5000 BC		5000-3200 BC		3200-750 BC		750 - 450 BC	450-50 BC	
South West Europe	9000 - 5500 BC		5500-3200 BC	3200-2250 BC	2250 - 750 BC		750 - 200 BC		
Spain	9000 - 5500 BC		5500-3200 BC	3200-2250 BC	2250 - 750 BC		750 - 200 BC		
Portugal	9000 - 5500 BC		5500-3200 BC	3200-2250 BC	2250 - 750 BC		750 - 200 BC		
Italy	9000 - 6000 BC		6000-3200 BC		3200-1000 BC		1000-300 BC		
South Eastern Europe	10000 - 6000 BC		6000 - 3200 BC		3200 - 2000 BC	2000-1100 BC	1100 - 600 BC		
Albania	10000 - 6000 BC		6000 - 2600 BC		2600 - 1800 BC	1800-1100 BC	1100 - 400 BC		
Bosnia and Herzegovina	10000 - 6000 BC		6000 - 3200 BC		3200 - 2000 BC	2000-1100 BC	1100 - 600 BC		
Bulgaria	10000 - 6000 BC		6000 - 3200 BC		3200 - 2000 BC	2000-1100 BC	1100 - 600 BC		
Croatia	10000 - 6000 BC		6000 - 3200 BC		3200 - 2000 BC	2000-1100 BC	1100 - 600 BC		
Greece	10000 - 6000 BC		6000 - 3200 BC		3200 - 2000 BC	2000-1100 BC	1100 - 600 BC		
Macedonia	10000 - 6000 BC		6000 - 3200 BC		3200 - 2000 BC	2000-1100 BC	1100 - 600 BC		
Moldova	10000 - 6000 BC		6000 - 3200 BC		3200 - 2000 BC	2000-1100 BC	1100 - 600 BC		
Romania	10000 - 6000 BC		6000 - 3200 BC		3200 - 2000 BC	2000-1100 BC	1100 - 600 BC		
Serbia	10000 - 6000 BC		6000 - 3200 BC		3200 - 2000 BC	2000-1100 BC	1100 - 600 BC		
Yugoslavia	10000 - 6000 BC		6000 - 3200 BC		3200 - 2000 BC	2000-1100 BC	1100 - 600 BC		
Southern Caucasus					3500-2400 BC	2400-1500 BC ; 1500-1150 BC	1150-300 BC		
Anatolia/ Caucasus				8000-3300 BC	3300-2000 BC	2000-1000 BC	1000-550 BC		500-331 BC

Country	ROMAN AGE							MIDDLE AGES		
	Archaic / Classical/ Urban	Hellenistic	Parthian	Roman Age	Roman Empire	Germanic Roman Age	Sasanian	Early Byzantium	Medieval Byzantium	Late Byzantium
British Isles				AD 1-400						
Ireland										
Northern and East Europe				AD 1-400						
Austria				AD 1-400						
Belarus				AD 1-400						
Czech Republic				AD 1-400						
Denmark				AD 1-400						
Estonia				AD 1-400		AD 400-800				
Finland				AD 1-400		AD 400-800				
Hungary				AD 1-400						
Latvia				AD 1-400		AD 400-800				
Lithuania				AD 1-400		AD 400-800				
Norway				AD 1-400		AD 400-800				
Poland				AD 1-400						
Russia				AD 1-400						
Slovakia				AD 1-400						
Slovenia				AD 1-400						
Sweden				AD 1-400		AD 400-800				
Ukraine				AD 1-400						
North West Europe				50 BC-AD 400						
Belgium				50 BC-AD 400						
France				50 BC-AD 400						
Germany				50 BC-AD 400						
Luxembourg				50 BC-AD 400						
Netherlands				50 BC-AD 400						
Switzerland				50 BC-AD 400						
South West Europe				200 BC-AD 400						
Spain				200 BC-AD 400						
Portugal				200 BC-AD 400						
Italy				300-27 BC	27 BC-AD 476					
South Eastern Europe	600-400 BC	400-168 BC		168 BC-AD 400				AD 400-800	AD 800-1250	AD 1250-1500
Albania	450-27 BC			27 BC-AD 395				AD 400-800	AD 800-1250	AD 1250-1500
Bosnia and Herzegovina	600-400 BC	400-168 BC		168 BC-AD 400				AD 400-800	AD 800-1250	AD 1250-1500
Bulgaria	600-400 BC	400-168 BC		168 BC-AD 400				AD 400-800	AD 800-1250	AD 1250-1500
Croatia	600-400 BC	400-168 BC		168 BC-AD 400				AD 400-800	AD 800-1250	AD 1250-1500
Greece	600-400 BC	400-168 BC		168 BC-AD 400				AD 400-800	AD 800-1250	AD 1250-1500
Macedonia	600-400 BC	400-168 BC		168 BC-AD 400				AD 400-800	AD 800-1250	AD 1250-1500
Moldova	600-400 BC	400-168 BC		168 BC-AD 400				AD 400-800	AD 800-1250	AD 1250-1500
Romania	600-400 BC	400-168 BC		168 BC-AD 400				AD 400-800	AD 800-1250	AD 1250-1500
Serbia	600-400 BC	400-168 BC		168 BC-AD 400				AD 400-800	AD 800-1250	AD 1250-1500
Yugoslavia	600-400 BC	400-168 BC		168 BC-AD 400				AD 400-800	AD 800-1250	AD 1250-1500
Southern Caucasus										
Anatolia/ Caucasus		331-133 BC	133 BC-233 AD				AD 223-622			

Country	MIDDLE AGES							MODERN	
	Early Islamic	Viking Period	Early Medieval Period	Middle Ages / Medieval Period	Later Islamic	Ottoman	Late Medieval	Renaissance	Early Modern
British Isles			AD 400-800	AD 800-1500					
Ireland									
Northern and East Europe			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Austria			AD 400-800	AD 800-1500					
Belarus			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Czech Republic			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Denmark		AD 800-1066	AD 400-800	1066-c.1500					
Estonia		AD 800-1066	AD 400-800	1066-c.1500					
Finland		AD 800-1066	AD 400-800	1066-c.1500					
Hungary			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Latvia		AD 800-1066	AD 400-800	1066-c.1500					
Lithuania		AD 800-1066	AD 400-800	1066-c.1500					
Norway		AD 800-1066	AD 400-800	1066-c.1500					
Poland			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Russia			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Slovakia			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Slovenia			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Sweden		AD 800-1066	AD 400-800	1066-c.1500					
Ukraine			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
North West Europe			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Belgium			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
France			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Germany			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Luxembourg			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Netherlands			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Switzerland			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
South West Europe			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Spain			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Portugal			AD 400-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
Italy			AD 476-800	AD 800-1250			AD 1250-1500	AD 1500-1650	AD 1650-1800
South Eastern Europe						AD 1500-1650			AD 1650-1800
Albania						AD 1500-1650			AD 1650-1800
Bosnia and Herzegovina						AD 1500-1650			AD 1650-1800
Bulgaria						AD 1500-1650			AD 1650-1800
Croatia						AD 1500-1650			AD 1650-1800
Greece						AD 1500-1650			AD 1650-1800
Macedonia						AD 1500-1650			AD 1650-1800
Moldova						AD 1500-1650			AD 1650-1800
Romania						AD 1500-1650			AD 1650-1800
Serbia						AD 1500-1650			AD 1650-1800
Yugoslavia						AD 1500-1650			AD 1650-1800
Southern Caucasus									
Anatolia/ Caucasus	AD 622-1258				AD 1250-1500	AD 1500-1920			

Sources: British Museum's World Timelines website (2010); James (2005); Project ArAGATS website run by Cornell University and the Institute of Archaeology and Ethnography, NAS, Armenia

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Appendix 4. References for zooarchaeological records of *Equus hydruntinus* and *E. hemionus*

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Appendix 6. Significant results of univariate analyses from General Linear Models (GLMs) across all chapters

CHAPTER 3

	Estimate	Standard error	t value	
(Intercept)	2.0177	0.3272	-6.1660	***
Trophic Guild (Herbivore)	1.6321	0.3926	4.1680	***
(Intercept)	-1.6722	0.2632	-6.3540	***
Diet breadth (Level 2)	0.9166	0.4590	1.9970	.
Diet breadth (Level 3)	0.8393	4.5299	0.1850	
Diet breadth (Level 5)	2.2634	0.5042	4.4890	***
Diet breadth (Level 6)	0.7079	0.6899	1.0260	
(Intercept)	-0.4192	0.2785	-1.5050	
Trophic level (Level 2)	0.0023	0.5335	0.0040	
Trophic level (Level 3)	-1.5216	0.4470	-3.4040	**

CHAPTER 5

	Estimate	Standard error	z value	
(Intercept)	-4.236	1.6259	-2.605	**
Log (body mass)	0.3953	0.1347	2.933	**
(Intercept)	6.93E-01	2.89E-01	2.401	*
Trophic level (Level 2)	-9.69E-13	5.77E-01	0	
Trophic level (Level 3)	-1.95E+00	7.64E-01	-2.548	*
(Intercept)	-0.2513	0.378	-0.665	
Diet (Level 2)	1.2629	0.4835	2.612	**
Diet (Level 5)	-17.0513	3467.8586	-0.005	

CHAPTER 6

	Estimate	Standard error	t value	
INTRINSIC FACTORS				
(Intercept)	-7.4085	1.806	-4.102	***
Log (body mass)	0.6557	0.1661	3.946	***
(Intercept)	1.1921	0.4917	0.0236	*
Trophic level 2	-2.0536	0.8308	-2.472	*
Trophic level 3	-2.2208	0.6444	-3.446	**
(Intercept)	1.1141	0.6569	0.1014	
Litter size	-0.6098	0.2845	0.0209	*
EXTRINSIC FACTORS				
(Intercept)	2.3237	0.6068	3.83	***
Log (HPD)	-0.4256	0.1338	-3.18	**
(Intercept)	-0.02797	0.17979	-0.123	

% forest cover	0.01447	0.00522	2.194	*
(Intercept)	-1.30085	0.61748	-2.107	*
Log (average elevation)	0.276	0.09768	2.826	**
Maximal model				
(Intercept)	0.62485	0.8843	0.707	
Log (HPD)	-0.36568	0.1284	-2.848	**
Log (average elevation)	0.22813	0.09288	2.456	*

* p < 0.05, ** p<0.01, *** p <0.001