Title: Mammalian tolerance to humans is predicted by body mass: evidence from long-term archives

Running Head: Body mass predicts mammalian decline

Jennifer J. Crees[1,2*]

Samuel T. Turvey[1]

Robin Freeman[1]

Chris Carbone[1]

[1]Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, UK
[2]Department of Earth Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK

*Email: j.crees@nhm.ac.uk

Abstract

Humans are implicated as a major driver of species extinctions from the Late Pleistocene to the present. However, our predictive understanding of human-caused extinction remains poor due to the restricted temporal and spatial scales at which this process is typically assessed, and the risks of bias due to “extinction filters” resulting from a poor understanding of past species declines. We develop a novel continent-wide dataset containing country-level last-occurrence records for 30 European terrestrial mammals across the Holocene (c.11,500 years to present), an epoch of relative climatic stability that captures major transitions in human demography. We analyze regional extirpations against a high-resolution database of human population density (HPD) estimates to identify species-specific tolerances to changing HPD through the Holocene. Mammalian thresholds to HPD scale strongly with body mass, with larger-bodied mammals experiencing regional population losses at lower HPDs than smaller-bodied mammals. Our analysis enables us to identify levels of tolerance to HPD for different species, and therefore has wide applicability for determining biotic vulnerability to human impacts. This ecological pattern is confirmed across wide spatiotemporal scales, providing insights into the dynamics of prehistoric extinctions and the modern biodiversity crisis, and emphasizing the role of long-term archives in understanding human-caused biodiversity loss.

Keywords: mammals, extinction filter, extinction risk, historical ecology, Holocene, human population density

Introduction

Humans are likely to have driven biodiversity loss for millennia, with anthropogenic activities widely considered to be responsible, at least in part, for global- and population-level extinctions from the end of the Pleistocene and across the Holocene up to the present

(MacPhee 1999; Turvey 2009; Faurby and Svenning 2015). Mammals in particular are highly susceptible to extinction from human activities such as hunting and habitat loss (Ripple et al. 2014; 2015). Understanding mammalian tolerance to human presence is therefore crucial for reconstructing the dynamics and drivers of historical and current extinctions, and predicting future biotic vulnerability to projected human population growth.

The sustainability of species' harvesting rates is linked strongly to body mass. Larger-bodied species typically have lower rates of reproduction than smaller species, and so rates of population increase typically decline with increasing body mass (Woodward et al. 2005). As a result, overharvesting is more likely to drive local extirpation or global extinction of larger-bodied species than smaller-bodies species (Brook & Bowman 2005; Zuo et al. 2013). Larger-bodied species also typically require bigger home ranges, making them more sensitive to habitat loss and bringing individuals into increased contact with people in fragmented habitats where they can be more vulnerable to offtake from hunting (Ripple et al. 2014; 2015). If levels of direct exploitation and habitat loss are both linked with human population density (HPD), we might expect that the regional presence of a species might be influenced by both its body mass and HPD.

There is already a body of ecological evidence associating HPD with patterns of mammalian persistence or extirpation (Woodroffe 2000; Karanth et al. 2010). However, such analyses are typically based only on recent ecological systems from which the most susceptible species have already become extinct due to past anthropogenic activity, with an "extinction filter" masking true patterns of species responses to human pressures (Faurby and Svenning 2015). Extinction is the end point of a potentially long-term process of cumulative population losses rather than a single, species-level event, and therefore it is vital to understand current-day mammal extinctions over wide spatiotemporal scales rather than studying past and present extinctions in isolation. For example, the aurochs (*Bos* *primigenius*), which became globally extinct in AD 1627, is often documented as the only European large mammal extinction following IUCN's cutoff of AD 1500 for assessing species extinctions (Temple and Terry 2007). However, this fails to acknowledge severe historical-era population-level losses in several other European mammal species, such as elk (*Alces alces*), European bison (*Bison bonasus*) and most of Europe's large carnivores (Crees et al. 2016), or earlier continent-level extinction of species such as lion (*Panthera leo*) and European wild ass (*Equus hydruntinus*) (Barnett *et al*. 2006; Crees and Turvey 2014). Extinction should therefore ideally be assessed at the regional landscape scale, as this is the spatial scale at which population losses occur (Crees et al. 2016).

The quality of long-term data for reconstructing past population distributions and dynamics is highly variable both spatially and temporally. However, Europe has a particularly well-resolved and detailed Holocene record documenting human and wild mammal occurrence in zooarchaeological deposits and historical archives from around 11,500 years ago to the present (e.g. Benecke 1999; Klein Goldewijk et al. 2010). Holocene Europe also encompasses several orders of magnitude of human activity, from small-scale, low-density hunter-gatherer communities to larger settled agricultural communities and recent industrialized and urbanized societies (Roberts 1998), thus capturing wide variation in human pressures on global environments, both historically and in the present. The broadly stable postglacial climate of the Holocene also allows documented mammal population and species losses to be more easily attributed to direct or indirect human activity compared to those during the more variable climatic conditions of the Late Pleistocene (Turvey 2009).

In order to investigate the relationship between human presence and mammal persistence through time we integrated datasets derived from the zooarchaeological and historical records to reconstruct regional extirpation chronologies for European mammals across the Holocene. By using long-term archives we remove the extinction filter of cumulative past population losses that can bias efforts to understand mammalian extinction dynamics from modern-day data alone. We combined these ecological archives with estimates of historical HPD available at a similar landscape-level spatial scale across Europe, to investigate patterns of species presence or absence in relation to body mass and HPD across space and time, and generate a new, predictive understanding of species-specific vulnerability to changing human pressures.

Methods

Data collection

We developed a novel dataset of country-level extirpations from 8000 BC to AD 2000 for all large terrestrial mammal species with a native Holocene range that occupied >5% of Europe's area (> 2 kg; n=30; Data S1: Table 1). This approach excluded range-restricted high-elevation species, and species for which Europe only represented the margin of their global range. A 2 kg body mass threshold represented the smallest body mass for which we were able to source regional last-occurrence data consistently (as the zooarchaeological and historical records are generally poorer for smaller-bodied species), but which also provided a sufficiently large dataset for robust analysis. Only native European mammal populations were included (i.e. excluding introduced populations of non-native species, and translocated or reintroduced populations of European species). Data were collected at the country level, as this constituted the finest spatial resolution that could be maintained consistently for all 30 species across millennial timescales given the quality and quantity of regional data from different sources. Data on regional extirpations were gathered from the zooarchaeological, historical and ecological literature using the most recent published information for each species. Where possible, data on country-level extirpations were verified from >1 independent data source (Data S1: Table 1).

Resolution of last-occurrence data ranged from specific calendar dates recorded in the recent historical literature (e.g. death of the last known aurochs in Poland in AD 1627), to the last known appearance of species in the zooarchaeological record associated with broader time intervals. Whilst many recent historical dates almost certainly represent the true date of the 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 fact that the youngest fossil found will rarely if ever represent the true last individual of a species (Signor and Lipps 1982). Where more than one zooarchaeological last-occurrence date was reported, the most recently published directly dated record was used. Vagrant individuals and/or transient populations were excluded unless there was reasonable evidence for establishment and/or breeding by AD 2000. For example, golden jackal (*Canis aureus*) has been intermittently recorded in Germany and the Czech Republic but with no 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 do appear to have become established in the past few decades, so these countries were included (Arnold et al. 2012). Where extinction-date information for a species was uncertain, data for those countries were omitted from the analysis. For example, the timing of extirpation of wild horse (*Equus ferus*) across many central European countries is very poorly understood due to its potential misidentification with domestic horse in the zooarchaeological record (Sommer et al. 2011), so data for these countries were excluded. The final number of species-country combinations totaled 541 (Data S1: Table 2).

Information on Holocene HPD was obtained from the HYDE global population database (Klein Goldewijk et al. 2010) from 8000 BC to AD 2000. Gridded HPD data (N/km^2) were extrapolated to country-level averages and logged. Mean HPD could be strongly influenced by high-density areas; however, our study is conducted across millennial timescales, when most human populations remained relatively mobile and were maintained at low densities. By contrast, highly concentrated areas of HPD such as large urban centers only arose in the last couple of centuries in Europe (Le Galès 2004). The time bins provided by the HYDE database were used to define a series of presence-absence records for each species in each country across the Holocene that were associated with a specific HPD (Data S1: Table 2).

Mammalian body mass data were taken from the PanTHERIA database (Jones et al. 2009) and logged for analysis. Data for the Asiatic wild ass (*Equus hemionus*) were used as a proxy for the closely related extinct *E. hydruntinus*, and data for domestic cattle (*Bos taurus*) were used for its wild ancestor *B. primigenius*, which is known to have experienced a size reduction in the Holocene to become comparable in mass to modern cattle (Wright and Viner-Daniels 2015).

Data analysis

In order to investigate species-specific thresholds of tolerance to HPD, we first analyzed individual species country-level presence-absence data using logistic regression (present~log10(hpd)), and calculated a “critical” human population density (CHPD) threshold for each species (i.e. the HPD at which a species would be predicted to become extinct across its range). CHPD thresholds were initially calculated at p = 0.5 following comparable studies investigating mammalian tolerance to HPD by e.g. Woodroffe et al. (2000). However, across our entire dataset there was a higher amount of presence data than absence data due to increased frequency of temporal sampling in the HYDE database towards AD 2000, as well as the removal of some early mammal extirpations (e.g. *Equus ferus* and *Felis silvestris*) from the final dataset due to poorer data quality. This resulted in a slightly imbalanced dataset containing relatively more presences for smaller extant species than absences for larger extinct species. To account for potential bias in the relative proportion of presence/absence data, we therefore also calculated individual species CHPDs using receiver operating characteristic (ROC) curves to determine optimum thresholds for all species models. A threshold of $p = 0.5$ biases models towards the larger subset (either presence or absence) whereas the use of ROC curves aims to balance sensitivity and specificity for models by finding the highest true positive rate together with the lowest false positive rate. Both sets of CHPD thresholds (those calculated at $p = 0.5$, and those calculated using ROC curves) are provided in Data S1: Table 3 for reference, but only those calculated using ROC curves are presented in Figure 2. Individual CHPD thresholds were then plotted against species body mass, and the scaling relationship between CHPDs and body mass was provided by a simple linear regression through the points (solid grey line and band, Figure 2). All estimates of slopes are presented ± 95% CI. Some extant species, such as Asian badger (*Meles leucurus*) and corsac fox (*Vulpes corsac*), had too few data points to calculate a CHPD threshold due to restricted distributions in Europe and so had to be excluded from analyses. The European wildcat (*Felis silvestris*) was also excluded due to poor quality of presence-absence data (Sommer and Benecke 2006). CHPD was also approximated for species that experienced no localized extirpations, using the 99th centile of the HPD in the countries where they were still present in AD 2000.

Presence-absence data for all species and countries were then also combined into a single continent-wide analysis that allowed us to incorporate both extinct and extant species and include those species which had very few absence points (e.g., Eurasian otter *Lutra lutra*), and which also explicitly explored the effects of life history variables in addition to HPD. Although several life history traits (e.g., reproductive rate) are likely to influence tolerance to HPD, we focused our analyses on the effects of variation in body mass, because these traits are strongly correlated with mass over such large size ranges of mammals (Jetz et al. 2004; Woodward et al. 2005). We also included trophic level (herbivore /carnivore) as a further predictor variable following the PanTHERIA database (Jones et al. 2009). Two species in our database (wild boar *Sus scrofa*; brown bear *Ursus arctos*) have broad omnivorous diets, so these species were assigned as herbivore and carnivore, respectively, due to low sample size for analysis (Bojarska & Selva 2012; Ballari & Barrios-García 2014). Other species-specific ecological variables such as home range and habitat association, which are known to be associated with variation in extinction vulnerability or resilience in modern-day mammal populations (Collen et al. 2011), could not be included in our analyses due to uncertainty over past Holocene conditions. For example, home range varies greatly across a species' geographic range, and modern-day home range estimates from outside Europe may not be representative of the ranging behavior of species historically present within Europe. Both mammalian species-specific habitat associations and the wider vegetational composition of European landscapes during the Holocene are also the subjects of continuing debate and uncertainty (e.g., Mitchell 2005; Hall 2008; Cromsigt et al. 2012; Fyfe et al. 2013).

We compared four models investigating the relationship between HPD and species body mass using logistic regression: (present~log10(hpd)), (present~log10(mass)), (present~log10(hpd)+log10(mass)), and (present~log10(hpd)*log10(mass)), where species and country were included as random effects. We also generated three further models exploring the additional potential impact of trophic level, included both as an additional and as an interaction term in different models (Data S1: Table 4). Models were ranked according to the Akaike Information Criteria (AIC), and the model with the lowest AIC value was interpreted as having the best explanatory power for explaining the influence of HPD and body mass on mammal presence-absence. All analyses were conducted using the glm and glmer packages MASS (Venables and Ripley 2004) and lme4 (Bates et al. 2015) in R3.0.2. (R Core Team 2017). We also used our continent-wide model to predict the maximum mammalian body mass that would be able to persist at different levels of HPD across the Holocene for two countries, UK and Norway, which are geographically proximate and experienced cultural transitions and patterns of agricultural intensification at similar times, but have contrasting high and low HPDs respectively.

Results

Humans have been a major driver of losses of European large mammal populations throughout the Holocene, with 209 recorded country-level extirpations across 22 species from around 4000 BC to AD 2000 (Figure 1; Data S1: Table 3). There were a higher number of country-level extirpations in north and northwest Europe, with Britain, Denmark and the Netherlands all losing over 60% of their original native Holocene large-bodied mammal fauna. However, human population pressures have not impacted species equally. We find a strong negative relationship (-0.61 ± 0.10, $p < 0.001$) between individual species' CHPD and body mass (Figure 2), with smaller species able to tolerate substantially higher HPDs than larger species. For example, golden jackal and Eurasian otter, which both have body masses below 10 kg, have persisted in areas with HPDs greater than 100 people/km^2, whilst aurochs and European bison, which have body masses between 650-800 kg and which have both now lost all of their native European populations, disappeared where HPDs were under 10 people/km^2. Using a phylogenetic generalized least squares approach to account for patterns of relatedness between species, we find the same slope and intercept as the simple linear regression and no clear phylogenetic signal (lambda = 0).

Using the continent-wide analysis, we find an even stronger relationship between body mass and HPD (-0.98, Figure 2). The model with the highest explanatory value is the one that includes interactions between HPD and body mass (see Data S1: Table 4 for model comparisons). The slope for this model is steeper than the slope through the individual species regressions, likely attributable to the fact that the explicit inclusion of body mass incorporates greater explanatory power and therefore reduces the amount of scatter around the slope. We found no significant improvement in our models based on AIC from the inclusion of trophic level (Data S1: Table 4). Similarly, those models that did include trophic level did not show any significant relationships of herbivory or carnivory on species presence/absence.

Our analysis of the maximum mammalian body mass that could be sustained in the UK and Norway shows a marked decline across the Holocene for both countries (Figure 3). The UK suffered a particularly substantial reduction in sustainable body mass around 1000 years ago, even though this was followed by a small increase associated with human population crash resulting from the Black Death in the 14th century AD. By AD 2000, Norway could theoretically sustain mammals with a body mass more than an order of magnitude higher than the UK due to its much smaller HPD. Our model accurately predicts a high sustainable mammal mass for Norway in the present day, including the size of its largest extant mammal species, e.g. European wolf (*Canis lupus*; 32 kg), brown bear (196 kg), and Eurasian elk (462 kg).

Discussion

Our study provides explicit evidence for a historical extinction filter that has selectively removed populations of large-bodied mammal species with lower tolerances to human presence from European landscapes from at least the Mid-Holocene onwards, far earlier than has typically been recognized. By using long-term archival data on past population losses we have been able to assess correlates of survival through time for Europe’s largest-bodied postglacial native mammals, many of which are now regionally extirpated. Due to their absence from current-day European faunas, these species are generally excluded from studies of extinction risk, but our historical analysis highlights their particularly low tolerance to human presence, whilst most smaller-bodied species have survived into the present across much or all of their ranges despite escalating growth of human populations. We have also calculated thresholds of mammalian tolerance to human populations over a millennial timescale and at regional spatial scales, and thus have been able to determine finer-scale responses to humans across time and space than studies focused on the present-day alone. We demonstrate that body mass and the HPD at which a mammal species becomes regionally extirpated are strongly interlinked, highlighting that larger-bodied mammals have been more vulnerable to human activity than smaller-bodied species even at low prehistoric levels of HPD, and supporting previous research which emphasizes that both intrinsic and extrinsic factors contribute towards extinction risk for larger mammals (Cardillo et al. 2005).

Humans have historically impacted mammal populations through a range of different direct and indirect processes, including hunting, habitat loss/degradation, and other processes such as introduced species/diseases, competition and/or hybridization with domestic mammals (Grayson 2001, Kaplan et al. 2009). These processes would undoubtedly have been accelerated by human population growth and the development of new technologies across the Holocene in Europe (Klein Goldewijk et al. 2011). However, the complex and staggered process of cultural and demic diffusion from the Neolithic onwards (e.g. Gkiasta et al. 2003) means that these effects would have varied both spatially and temporally, and so are difficult to analyze directly in relation to mammal population losses. Yet the strong statistical relationship between HPD and mammal population loss, shown in both our species-specific and continent-wide models, demonstrates that this general index of human activity can actually represent a reliable proxy for anthropogenic pressure through time, despite the complex nature of human societal development. Our analysis may therefore constitute a useful tool for identifying scenarios where particular mammal species are likely to be vulnerable to anthropogenic pressures either now or in the future, without necessarily requiring more detailed data on the type of human-wildlife interaction. This study may be particularly useful and timely given continued forecasts for global human population growth (Bradshaw and Brook 2014). Our findings also highlight the extreme vulnerability of large mammals in particular to humans, regardless of the type of anthropogenic activity they are exposed to, and provide support for the importance of maintaining global wilderness areas of low human density for such species (Watson et al. 2016).

Incorporating baselines from long-term ecological archives requires the use of centennial-scale or millennial-scale historical data, which are inevitably somewhat imprecise. Our country-level mammalian last-occurrence records typically represent *terminus post quem* dates, providing an earliest possible boundary date for regional extinction rather than an absolute extinction date, and HPDs derived from the HYDE database are modeled estimates. However, because both of these sets of data become increasingly well resolved and precise closer to the present, they are of a comparable resolution for the purposes of analysis. Similarly, because of the relatively broad temporal and spatial resolution of our historical data, we chose to focus on the effects of body mass, a commonly-used biological characteristic which is highly likely to act as a surrogate for other key life-history traits that may be driving extinction patterns (Woodward et al. 2005). For example, slow reproductive rate rather than large body mass has been shown to be a key direct driver of late Quaternary mammal extinctions, but these traits exhibit strong collinearity (Johnson 2002). Future research could therefore investigate a more specific series of life-history traits associated with historical patterns of extinction and how these interact with HPD. Nonetheless, given the unavoidable issues of resolution and precision associated with the use of historical datasets, the clarity and consistency of our results is encouraging. This highlights the strength of the relationship we detect between mammal extirpation and HPD, and supports increased use of zooarchaeological and historical archives for reconstructing long-term spatial and temporal extinction dynamics (Turvey et al. 2015; Crees et al. 2016).

Some European mammal species do currently survive in countries with HPDs above their predicted thresholds. This “mismatch” may be due primarily to either finer-scale regional heterogeneity in HPD and environmental characteristics such as topography, which was not accounted for at the country-level spatial scale at which we conducted our analyses (e.g. remnant populations often persist in high-elevation refugia; Fisher 2011, Turvey et al. 2015), or more recent management and local maintenance of populations of large-bodied species for conservation or hunting (Dickson et al. 2009). For example, red deer (*Cervus elaphus*; 241 kg) and roe deer (*Capreolus capreolus*; 23 kg) both remain widespread in the UK, where we predict a body mass threshold of between 3.6 and 17.1 kg (for HPD of 203 people/km^2, Figure 2), but these deer species are heavily managed (Ward 2005). Likewise, although several large carnivores such as wolf, brown bear and lynx (*Lynx lynx*) still persist in several central European countries such as France, Switzerland, Austria and Italy, they are almost exclusively restricted to remnant populations in montane areas (e.g. the Alps, Appenines and Pyrenees) where HPD is far lower than elsewhere in these countries; however, they now exist at very low densities even in these high-elevation regions (Kaczensky et al. 2012). Legal protection and active attempts to foster co-existence between people and wildlife have also facilitated mammal recovery in some regions of Europe, offsetting high human presence (Deinet et al. 2013, Chapron et al. 2014). Ideally our analysis would therefore benefit from being undertaken at even finer spatial scales in order to capture more precise species-specific HPD thresholds. Unfortunately, however, historical and zooarchaeological data on patterns of persistence and extinction of different mammal populations would be difficult if not impossible to obtain consistently across many species below the country level. It should also be noted that we only investigated mammalian extirpation and HPD up to AD 2000 in this study. Therefore, for species that experienced no regional extirpations by this time, the 99th centile of the HPD across their range at this date was used. As such, thresholds for these species may better be viewed as minimum estimates of tolerance to HPD.

Although we found no additional relationship between mammalian tolerance to humans and trophic level, our long-term historical analysis of individual species has highlighted that due to their large size, many formerly widespread ungulate taxa—in particular Europe's bovids and equids—have been highly susceptible to extirpation by humans in the past (Figure 2). However, due to their relatively early extirpation, these are also paradoxically the species most likely to be subject to an extinction filter. Indeed, the European wild ass has been largely forgotten as a member of Europe's former Holocene large mammal fauna, as it is only known from the zooarchaeological record rather than from verified historical reports (Crees and Turvey 2014). Large-bodied ungulates are likely to be particularly vulnerable to human pressures for several reasons: their slow reproduction renders them intrinsically vulnerable to overharvesting, but they are a key target of hunting for food by human populations, and their dependence on primary productivity means that large tracts of land are required to support populations of grazing and browsing herbivores (Ripple et al. 2015). Any landscape-scale changes, including not only wide-scale habitat loss and degradation, but also competition from livestock, will therefore reduce food availability to support large ungulate populations, and such changes are documented across Holocene Europe from as early as 1000 BC (Kaplan et al. 2009; Klein Goldewijk et al. 2010). Major grassland and open forest habitats also tend to be distributed in lowland areas, and European ungulates show elevational niche differentiation between lowland and highland specialists. By contrast, even large-bodied carnivores can exploit a range of landscapes and elevations, and their ability to prey switch may also enable them to persist in marginal and degraded habitat, or in areas unsuitable for maintaining large human populations (Ripple et al. 2014). Unlike herbivores, some carnivores have more recently adapted to living in the margins of urban and suburban environments. However, these carnivore species are almost exclusively medium-size predators with generalist diets, and those that are larger and more strictly carnivorous tend to come into more direct conflict with humans (Bateman and Fleming 2012).

The Holocene is an important period in human history, capturing extensive and relatively rapid changes in activity and population demographics (Roberts 1998). However, these changes have not been uniformly distributed through time or space, either in Europe or at a global scale, and a wide range of human subsistence, settlement, and population density patterns continue to exist today. The results of this study are therefore also relevant to understanding and managing modern mammal coexistence with humans, as well as responses to human pressures in historical populations. For example, our analysis could help to identify species or populations that may face the highest threat of extirpation associated with either current-day human population density or future human population growth. In addition, it could aid identification of landscapes that have already exceeded HPD thresholds and that have accumulated “extinction debts” of species or populations that are unviable in the long-term in the absence of targeted conservation intervention (Kuussaari et al. 2009).

Geographic variation in human demographic projections suggests that the future status of large mammals may be mixed across Europe. Human population is expected to decrease ~25-50% by 2080 across much of eastern and central Europe, from Lithuania in the north to Bulgaria and Greece in the south (Eurostats 2019), and the likelihood of agricultural land abandonment by 2030 is also highest in these regions (Perpiña Castillo et al. 2018). These projected changes could present multiple opportunities for further large mammal recovery in the face of declining human populations and associated pressures (Deinet et al. 2013). By contrast, human populations are projected to increase ~25-50% in areas of western and northern Europe such as Britain, Scandinavia, and the Benelux countries (Eurostats 2019), potentially increasing human-mammal encounters and conflict; however, these countries are also expected to have over 90% of their human populations living in urban areas by 2050, the highest proportions in Europe (United Nations 2018). The shift in concentration of human density to urban spaces may therefore alleviate pressures on large mammals even in the most highly populated countries.

Information on historical HPD thresholds may also be useful in targeting suitable landscapes for species rewilding, and to anticipate the likelihood of survival for different species within proposed reintroduction sites (Seddon et al. 2014). The use of past data also highlights that in the absence of modern conservation action that can reverse negative effects of human-wildlife interaction, large-bodied mammals have historically been extremely vulnerable to even relatively low human populations, and even in the absence of technologically advanced hunting methods.

Our study uniquely uses an empirical late Quaternary data-driven approach to demonstrate and define the negative relationship between species body mass and tolerance to HPD, to better understand how larger-bodied species are increasingly vulnerable to human impacts. Using an extensive new dataset of mammalian regional extirpations across the entire Holocene Epoch and at a continental scale, we introduce an analytical framework that can identify species-specific HPD thresholds for extinction across a wide range of mammal taxa. These findings highlight the importance of using long-term historical and even prehistoric datasets to better understand the full extent of past human impacts on global mammal faunas, in order to contribute to a conservation evidence-base that will help to protect threatened populations into the future.

Acknowledgements

Funding was provided by a Natural Environment Research Council Grant (NE/G011745/1) and a Royal Society University Research Fellowship (UF080320/130573).

References

Arnold, J., A. Humer, M. Heltai, D. Murariu, N. Spassov, and K. Hacklaender. 2012. Current status and distribution of golden jackals *Canis aureus* in Europe. Mammal Rev 42:1-11.

Ballari, S. A., and M. N. Barrios-García. 2014. A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. Mammal Rev 44:124-134.

Barnett, R., N. Yamaguchi, I. Barnes, and A. Cooper. 2006. The origin, current diversity and future conservation of the modern lion (*Panthera leo*). Proc Roy Soc B 273:2119-2125.

Bateman, P. W., and P. A. Fleming. 2012. Big city life: carnivores in urban environments. J Zool 287:1-23.

Bates, D. M. Maechler, B. Bolker, and S. Walker 2015. Fitting linear mixed-effects models using lme4. J Stat Softw 67:1-48.

Benecke, N. 1999, The Holocene history of the European vertebrate fauna: modern aspects of research: Archäologie in Eurasien, Bd. Rahden/Westf., Verlag Marie Leidorf GmbH.

Bojarska, K., and N. Selva. 2012. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. Mammal Rev 42:120-143.

Bradshaw, C. J., and B. W. Brook. 2014. Human population reduction is not a quick fix for environmental problems. Proc Natl Acad Sci U S A 111:16610-16615.

Brook, B. W., and D. M. Bowman. 2005. One equation fits overkill: why allometry underpins both prehistoric and modern body size-biased extinctions. Popul Ecol 47:137-141.

Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. Bininda-Emonds, W. Sechrest, C. D. L. Orme et al. 2005. Multiple causes of high extinction risk in large mammal species. Science 309:1239-1241.

Chapron, G., et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:1517-1519.

Collen, B., L. McRae, S. Deinet, A. De Palma, T. Carranza, N. Cooper, J. Loh, and J. E. M. Baillie. 2011. Predicting how populations decline to extinction. Phil Trans Roy Soc B 366:2577-2586.

Crees, J. J., C. Carbone, R. S. Sommer, N. Benecke, and S. T. Turvey. 2016. Millennial-scale faunal record reveals differential resilience of European large mammals to human impacts across the Holocene Proc Roy Soc B 283:20152152.

Crees, J. J., and S. T. Turvey. 2014. Holocene extinction dynamics of *Equus hydruntinus*, a late-surviving European megafaunal mammal. Quat Sci Rev 91:16-29.

Cromsigt, J. P. G. M., G. I. H. Kerley, and R. Kowalczyk. 2012. The difficulty of using species distribution modelling for the conservation of refugee species – the example of European bison. Divers Distrib 18:1253-1257.

Deinet, S., C. Ieronymidou. L. McRae, I. J. Burfield, R. P. Foppen, B. Collen, and M. Böhm. 2013. Wildlife comeback in Europe: the recovery of selected mammal and bird species. Final report to Rewilding Europe by ZSL, BirdLife International and the European Bird Census Council. Zoological Society of London.

Dickson, B., J. Hutton, and W. A. Adams. 2009, Recreational hunting, conservation and rural livelihoods: science and practice. John Wiley & Sons.

Eurostat. 2019. Population. Retrieved from http://appsso.eurostat.ec.europa.eu/nui/show.do?dataset=proj_15npms&lang=en.

Faurby, S., and J. C. Svenning. 2015. Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns. Divers Distrib 21:1155-1166.

Fisher, D. O. 2011. Trajectories from extinction: where are missing mammals rediscovered? Glob Ecol Biogeogr 20:415-425.

Fyfe, R. M., et al. 2013. The Holocene vegetation cover of Britain and Ireland: overcoming problems of scale and discerning patterns of openness. Quat. Sci. Rev. 73:132-148.

Gkiasta, M. T. Russell, S. Shennan, and J. Steele. 2003. Neolithic transition in Europe: the radiocarbon record revisited. Antiquity 77:45-62.

Grayson, D. K. 2001. The archaeological record of human impacts on animal populations. J World Prehist 15:1-68.

Hall, S. J. G. 2008. A comparative analysis of the habitat of the extinct aurochs and other prehistoric mammals in Britain. Ecography 31:187-190.

Jetz, W., Carbone, C., Fulford, J., & Brown, J. H. 2004. The scaling of animal space use. Science 306:266-268.

Jones, K. E., J. Bielby, M. Cardillo, S. A. Fritz, J. O'Dell, C. D. L. Orme, K. Safi et al. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90:2648.

Kaczensky, P., G. Chapron, M. von Arx, D. Huber, H. Andrén, and J. Linnell. 2013, Status, management and distribution of large carnivores - bear, lynx, wolf & wolverine - in Europe. European Commission.

Kaplan, J. O., K. M. Krumhardt, and N. Zimmermann. 2009. The prehistoric and preindustrial deforestation of Europe. Quat Sci Rev 28:3016-3034.

Karanth, K. K., J. D. Nichols, K. U. Karanth, J. E. Hines, and N. L. Christensen. 2010. The shrinking ark: patterns of large mammal extinctions in India. Proc Roy Soc B 277:1971-1979.

Klein Goldewijk, K., A. Beusen, and P. Janssen. 2010. Long-term dynamic modeling of global population and built-up area in a spatially explicit way: HYDE 3.1. The Holocene 20:565-573.

Klein Goldewijk, K., A. Beusen, G. van Drecht, and M. de Vos. 2011. The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. Global Ecol Biogeogr 20:73-86.

Le Galès, P. 2002. European cities: social conflict and governance. Oxford: OUP.

MacPhee, R. D. 2009. Extinctions in near time: causes, contexts, and consequences. Springer.

Mitchell, F. J. G. 2005. How open were European primeval forests? Hypothesis testing using palaeoecological data. J Ecol 93:168-177.

Perpiña Castillo, C., B. Kavalov, V. Diogo, C. Jacobs-Crisioni, F. Batista e Silva, and C. Lavalle. 2018. Agricultural land abandonment in the EU within 2015-2030. Ispra, Italy: JRC Policy Highlights, European Commission.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger et al. 2014. Status and ecological effects of the world's largest carnivores. Science 343:1241484.

Ripple, W. J., T. M. Newsome, C. Wolf, R. Dirzo, K. T. Everatt, M. Galetti, M. W. Hayward et al. 2015. Collapse of the world's largest herbivores. Science Advances 1:e1400103.

Roberts, N. 2013, The Holocene: an environmental history, John Wiley & Sons.

Seddon, P. J., C. J. Griffiths, P. S. Soorae, and D. P. Armstrong. 2014. Reversing defaunation: restoring species in a changing world. Science 345:406-412.

Signor, P. W., and J. H. Lipps. 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. Geol Soc Spec Pap 190:291-296.

Sommer, R., and N. Benecke. 2006. Late Pleistocene and Holocene development of the felid fauna (Felidae) of Europe: a review. J Zool 269:7-19.

Sommer, R. S., N. Benecke, L. Lõugas, O. Nelle, and U. Schmölcke. 2011. Holocene survival of the wild horse in Europe: a matter of open landscape? J Quat Sci 26:805-812.

Temple, H. J., and A. Terry. 2007. The status and distribution of European mammals. IUCN Species Programme.

Turvey, S. T. 2009. Holocene extinctions. Oxford: Oxford University Press.

Turvey, S. T., J. J. Crees, and M. M. Di Fonzo. 2015. Historical data as a baseline for conservation: reconstructing long-term faunal extinction dynamics in Late Imperial–modern China Proc Roy Soc B 282:20151299.

United Nations, Department of Economic and Social Affairs, Population Division. 2018. World urbanization prospects: the 2018 revision. Online edition. Retrieved from https://population.un.org/wup/Download/.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Fourth edition. Springer.

Ward, A. I. 2005. Expanding ranges of wild and feral deer in Great Britain. Mammal Rev 35:165-173.

Watson, J. E., D. F. Shanahan, M. Di Marco, J. Allan, W. F. Laurance, E. W. Sanderson, B. Mackey et al. 2016. Catastrophic declines in wilderness areas undermine global environment targets. Curr Biol 26:2929-2934.

Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. Anim Conserv 3:165-173.

Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. Trends Ecol Evol 20:402-409.

Wright, E., and S. Viner-Daniels. 2015. Geographical variation in the size and shape of the European aurochs (*Bos primigenius*). J Arch Sci 54:8-22.

Zuo, W., F. A. Smith, and E. L. Charnov. 2013. A life-history approach to the late Pleistocene megafaunal extinction. Am Nat 182:524-531.

Figure 1. Number of species (left plot); human population density (N/km2) (middle plot); maximum sustainable body mass (kg) (right plot) for each European country at AD 1, AD 1000, AD 1500 and AD 2000.

Figure 2. Individual estimates of critical human population density (N/km^2 ±95% CI) of 22 mammal species against body mass (kg) (black points) calculated using receiver operating characteristic (ROC) curves (Data S1: Table 2). Estimated upper (99th centile) human population densities at AD 2000 shown for species that have experienced no recorded country-level extirpations (grey points). All values are logged. Solid grey line and band represent a simple linear regression fit through individual species thresholds $\widehat{\mathrm{N}}_{\mathrm{h}}$ (±95% CI). Dotted grey line represents the optimum general linear model fit given by the full continent-wide analysis including all presence-absence data and incorporating interactions between HPD and body mass. The wildcat (*Felis*) was an outlier (open circle point) and was excluded from analysis (see Methods).

Figure 3. Predicted maximum body mass thresholds (kg) for the United Kingdom (red line and points) and Norway (blue line and points) using estimated human population densities from 8000 BC to 2000 AD. Predicted mass was capped at 1000 kg.

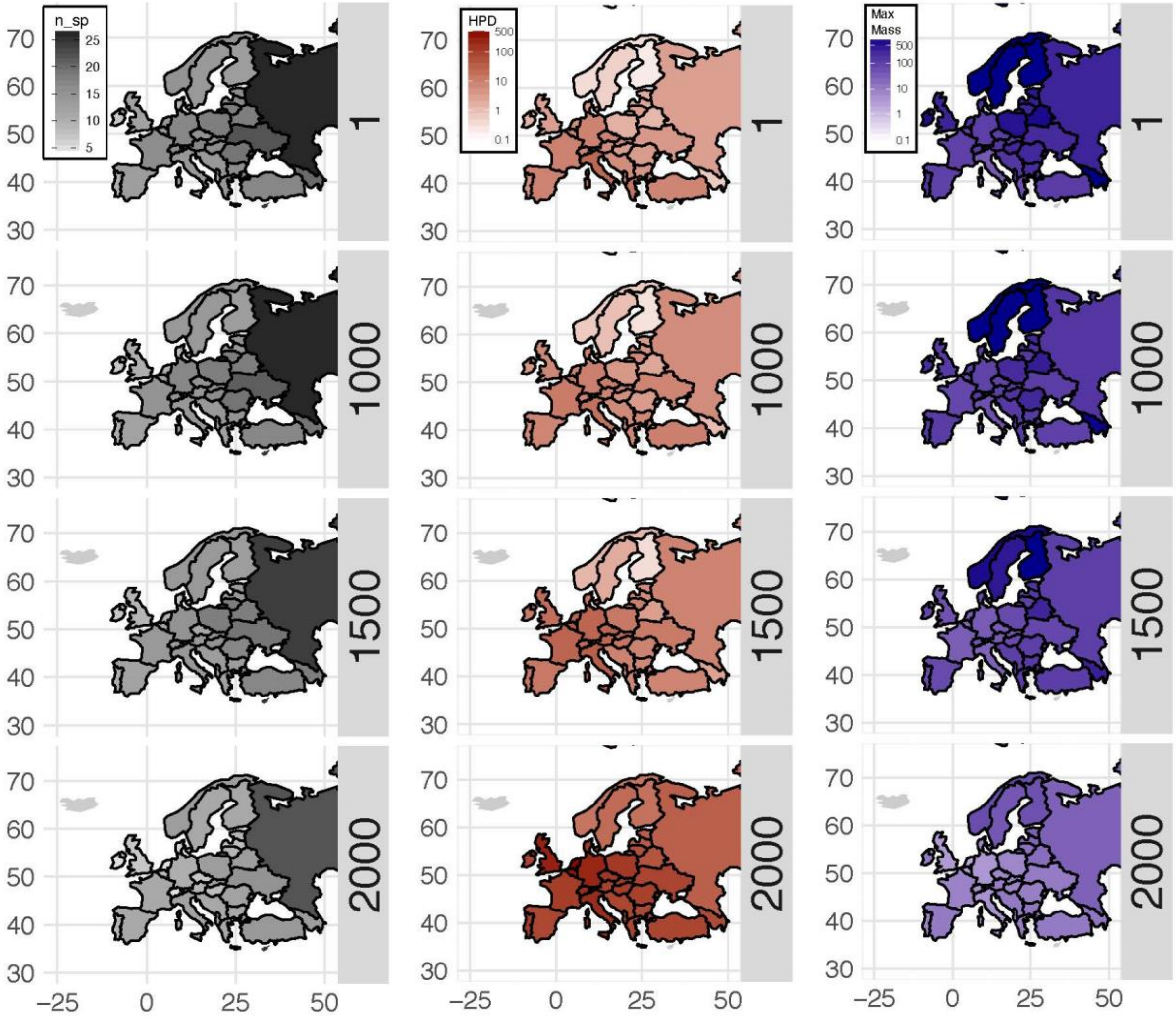
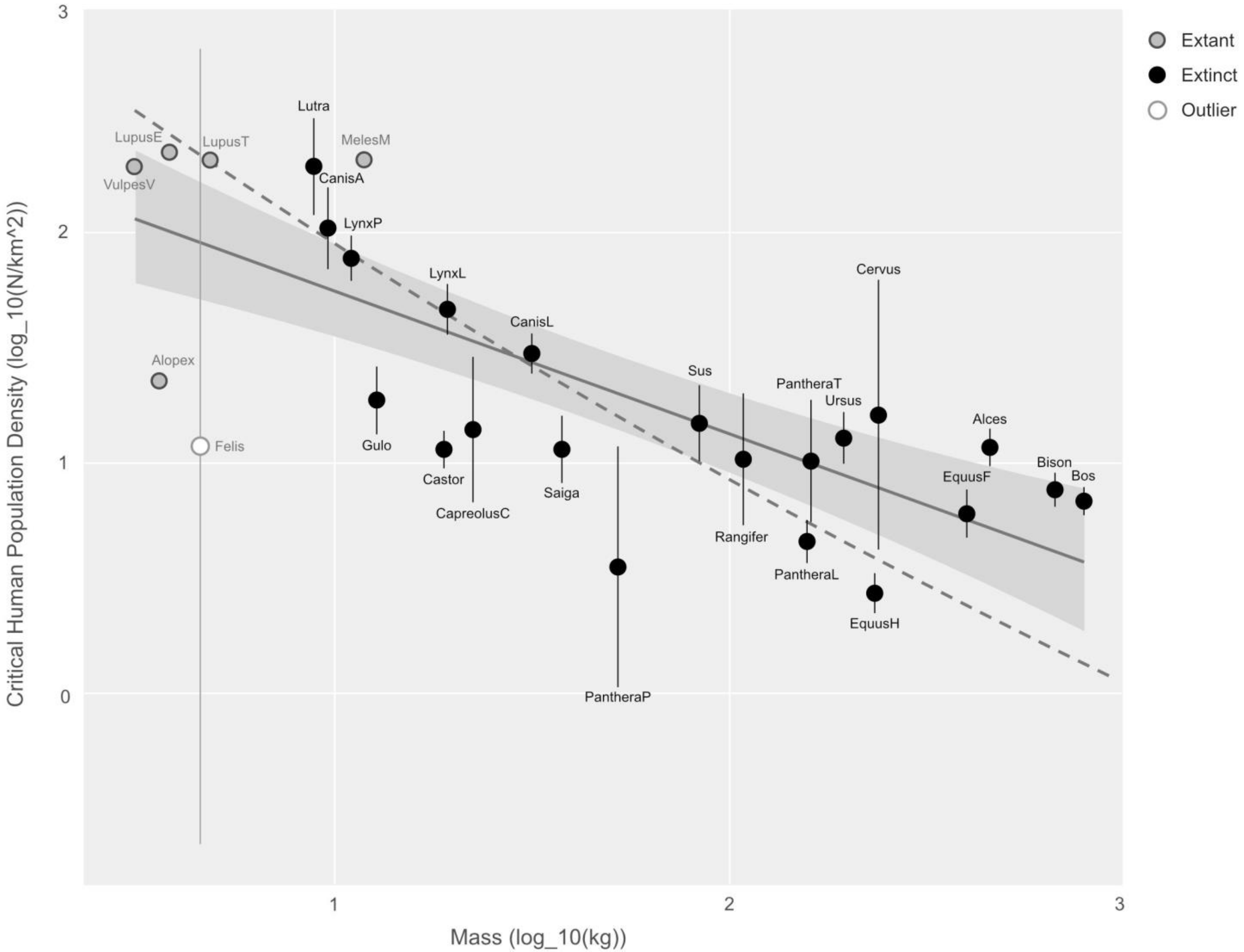
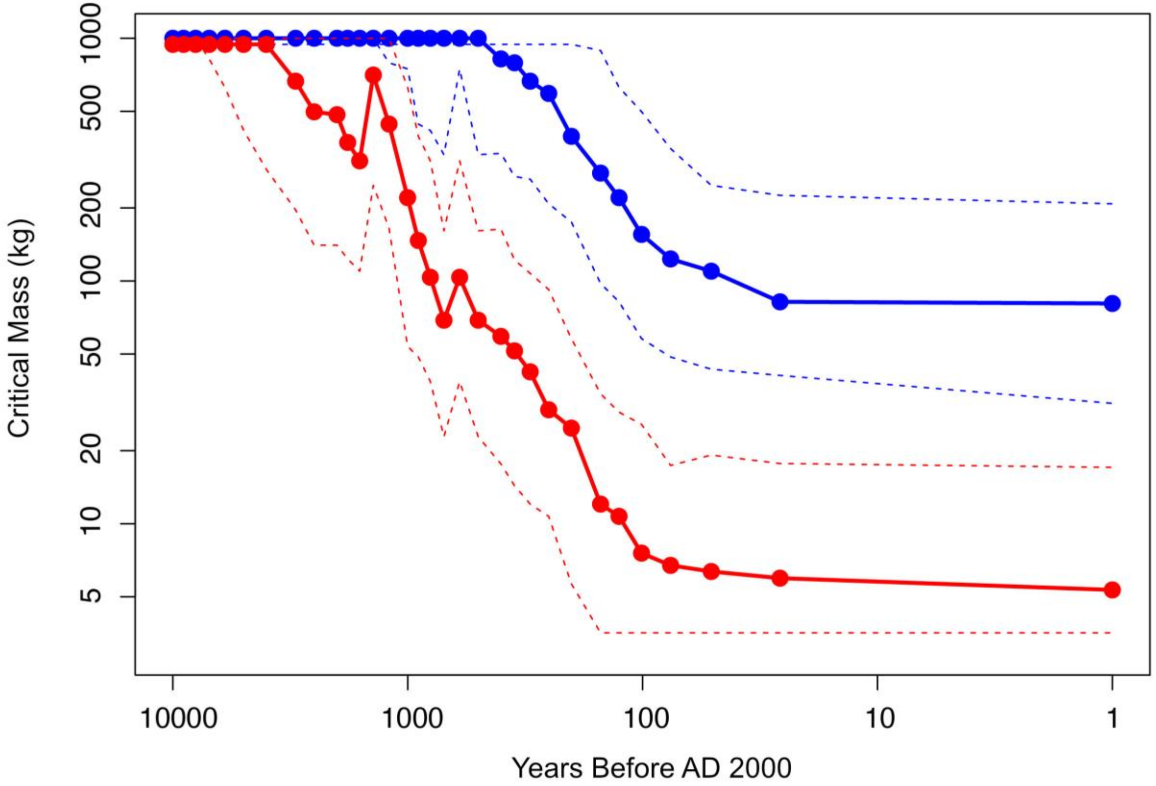

n_sp
25
20
15
10
5
HPD
500
100
10
1
0.1
Max
Mass
500
100
10
1
0.1
70
60
50
40
30
−25
0
25
50
1
1000
1500
2000

Figure 1



569

570 Figure 2



571

572 Figure 3