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Holocene extinction dynamics of *Equus hydruntinus*, a late-surviving European megafaunal mammal

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ABSTRACT

The European wild ass (*Equus hydruntinus*) is a globally extinct Eurasian equid. This species was widespread in Europe and southwest Asia during the Late Pleistocene, but its distribution became restricted to southern Europe and adjacent geographic regions in the Holocene. Previous research on *E. hydruntinus* has focused predominantly on its taxonomy and Late Pleistocene distribution. However, its Holocene distribution and extinction remain poorly understood, despite the fact that the European wild ass represents one of Europe's very few globally extinct Holocene megafaunal mammal species. We summarise all available Holocene zooarchaeological spatio-temporal occurrence data for the species, and analyse patterns of its distribution and extinction using point pattern analysis (kernel density estimation and Clark Evans index) and optimal linear estimation. We demonstrate that the geographic range of *E. hydruntinus* became highly fragmented into discrete subpopulations during the Holocene, which were associated with separate regions of open habitat and which became progressively extinct between the Neolithic and Iron Age. These data challenge previous suggestions of the late survival of *E. hydruntinus* into the medieval period in Spain, and instead suggest that postglacial climate-driven vegetational changes were a primary factor responsible for extinction of the species, driving 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.

1. 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 (Coard and Chamberlain, 1999; Benecke, 1999a). However this process did not occur entirely uniformly across Europe due to climatic variation and the existence of habitat 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 open habitat adapted megafaunal mammal species, including woolly mammoth (*Mammuthus primigenius*), giant deer (*Megaloceros giganteus*) (Stuart, 1999; Stuart et al., 2004), musk ox (*Ovibos moschatus*), reindeer (*Rangifer tarandus*) and wild horse (*Equus ferus*) (Macphee et al., 2002), persisted into the Holocene in different regions of northern Eurasia. The European wild ass (*Equus hydruntinus*) is another such megafaunal mammal species that persisted in Eurasia until the mid-late Holocene. This species is one of the most poorly understood representatives of the Late Pleistocene Eurasian mammal megafauna, despite surviving until much more recently than most other globally extinct large-bodied mammals. This is partly due to the relatively small number of available fossil or zooarchaeological records in comparison to other Late Quaternary megafaunal mammals, but also due to taxonomic confusion over its species status that is still being resolved. However, as one of the relatively few now-extinct megafaunal survivors of the Pleistocene–Holocene transition in Eurasia, this species has the potential to yield important new insights into end-Pleistocene megafaunal extinction dynamics and the nature of faunal response to climatic and anthropogenic impacts.

E. hydruntinus was first described by Regalia (1907) on the basis of fragmentary material from southern Italy, and was further described by Stehlin and Graziosi (1935) using fossils from the Upper Palaeolithic Romanelli cave site in the same

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region. These authors compared the anatomy of asses (African 'true' asses) and hemiones (Asian 'half-asses') and argued that the Romanelli fossils displayed a mixture of characteristics from both taxonomic groups. More recently, Burke et al. (2003) confirmed that *E. hydruntinus* shares morphological traits with numerous Old World Late Quaternary equids other than horses; for example, it has limb bone proportions most similar to those of hemiones and upper teeth more like asses, whilst its lower teeth are more similar to the extinct *E. stenonis*. *E. hydruntinus* can be characterised by a combination of small teeth, upper cheek teeth with small protocones, lower cheek teeth with a double asinine loop, molars with a long buccal groove, and slender limb bones (Eisenmann and Patou, 1980; Burke et al., 2003).

It has recently 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 hemione species, whereas ancient DNA analyses have argued that it may have been a subspecies of the extant Asiatic wild ass or onager (*Equus hemionus*) (Orlando et al., 2009; Geigl and Grange, 2012). However, Orlando et al. (2009) also noted that the onager and kiang (*E. kiang*) show poor mitochondrial differentiation yet can be classified as separate species on the basis of coat colour and other morphological characteristics, geographic distribution, and number of chromosomes. Although further molecular analysis, especially of nuclear loci, would help to clarify the taxonomic status of *E. hydruntinus*, the available data therefore indicate that it may indeed represent a distinct, recently extinct equid species.

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). This distribution reflected its ecological dependence upon the open landscapes that predominated across Eurasia during the Late Pleistocene (Huntley et al., 2013), similar to other megafaunal mammals including cave lion (*Panthera spelaea*) (Stuart and Lister, 2011), cave bear (*Ursus spelaeus*) (Pacher and Stuart, 2009), giant deer (Stuart et al., 2004) and woolly mammoth (Stuart et al., 2002. Further east, *E. hydruntinus* was replaced ecologically by Asian hemione species.

The Holocene distribution of *E. hydruntinus* has up until now largely been discussed in the context of specific localities associated with particular specimens or records of interest. Notably, Antunes (2006) suggested that *E. hydruntinus* may have survived into the thirteenth century AD in Portugal and the sixteenth century AD in southeastern Spain. He argued that the mediaeval word 'zebro', referring to an animal resembling a hemione that was mentioned in forais (mediaeval charters) and used as the basis of numerous toponyms in Portugal, in fact referred to the European wild ass. However, wider-scale Holocene spatial and temporal distribution data have not been synthesised for the species, making it difficult either to assess the likelihood that 'zebro' could indeed refer to a late-surviving population of European wild ass, or to address questions with wider relevance for understanding Late Quaternary megafaunal ecology such as the spatial response of *E. hydruntinus* to end-Pleistocene climate change, the correlates of its Holocene range, or the dynamics or timing of its eventual extinction. A closer examination of the available Holocene data for *E. hydruntinus* within a quantitative analytical framework may therefore contribute towards a better understanding of the distribution and range decline of this species 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.

2. Materials and methods

2.1. Data collection

All Holocene records of *E. hydruntinus* that could be located were sourced from the literature, including both journal articles and grey literature, using Web of Science, Google Scholar and library searches. As much of the literature did not appear in mainstream sources, many references were found within articles on the species. Unpublished data from Armenia were obtained from the Institute of Zoology in Yerevan (Ninna Manaserian, personal communication, April 2011). Records of *E. hemionus* from across the same geographic region were also compiled to investigate whether the two taxa were allopatric or sympatric across any parts of their respective ranges. If these two equids did reportedly overlap in range, then zooarchaeological identification must be undertaken carefully in these regions and, where identifications appear uncertain, records treated with caution. The number of records of *E. hydruntinus* was also compared with those of other ungulates in Holocene Europe, extracted from a wider European mammal fauna database (Benecke, 1999a; supplemented by; Crees, 2013). Information was compiled on each geographic 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). Uncalibrated radiocarbon records were calibrated using the calibration curve IntCal 09 in the programme OxCal version 4.1 (Bronk Ramsey, 2009). As no dating method in archaeology can return a single date, all records were treated as estimated interval dates. Dates related to cultural periods were taken from the literature, and dates of archaeological periods were compiled following the British Museum's World Timelines website (2010), with specific dates for the Caucasus region taken from the Project ArAGATS website run by Cornell University and the Institute of Archaeology and Ethnography, National Academy of Sciences of Armenia (2010). More detailed information on dating of zooarchaeological records taken from the literature is given in Crees (2013). 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.

2.2. Spatial analysis

Point pattern analysis (Lloyd, 2010) was carried out using the statistical package R version 0.96.122 (RStudio, 2012) to investigate the spatial spread of Holocene distribution data for *E. hydruntinus*, and to analyse whether this distribution shows evidence of fragmentation. Point pattern analysis is widely used in spatial analyses, for example in epidemiology and increasingly in ecology, to study population distributions of species. Firstly, kernel density estimation was conducted using the R package *spatstat*, to investigate the spread and intensity of points across the sampled region. This package computes a fixed-bandwidth kernel estimate of the intensity of the point process that generated the pattern, revealing variations in intensity of occupation of different areas and therefore the spatial distribution of a species across a landscape (Bivand et al., 2008). Secondly, a simple aggregation index, the Clark Evans index, was used 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), i.e. where the null hypothesis is Complete Spatial Randomness (CSR). A value of $R > 1$ indicates spatial ordering, while $R < 1$ indicates spatial clustering. These combined approaches permitted estimation of the approximate geographic distribution of