Glacial and post-glacial adaptations of hunter-gatherers: Investigating the late Upper Paleolithic and Mesolithic subsistence strategies in the southern steppe of Eastern Europe

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Diverse landscapes and ecosystems stretching across Europe led to diverse hunter-gatherer cultural records during the Upper Paleolithic and Mesolithic. In response to abrupt climatic forcing, starting around the Late Glacial Maximum and followed by climatic events such as the Bolling–Allerød and the Younger Dryas in the Terminal Pleistocene, archaeological data pertaining to cultural and behavioral shifts of hunter-gatherers continue to be explored on a regional and pan-regional scale. Here we present an initial summary, which includes new and published data on faunal analyses from multiple open air sites that span the Late Pleistocene to the Holocene, dated between the Late Upper Paleolithic and Mesolithic (20,000–6000 uncal 14C BP) in the southern steppe of Eastern Europe. For this area, this is the first study to compile the cultural and faunal data with geo-referenced localization and radiometric dates of the archaeological sites. Taken together, faunal assemblages from the Epigravettian are characterized by low diversity and are often dominated by one species of large game, including bison and equids, whereas the Mesolithic diet is characterized by higher inter-site variability subsisting on large ungulate and greater emphasis on freshwater resources. This study contributes to the general knowledge concerning the last phases in the evolution of the Eurasian hunter-gatherers.

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1. Introduction

The past adaptation of Paleolithic and Mesolithic hunter-gatherers in Europe is a result of their interaction with the diverse landscapes and ecosystems. Unlike other cultural transitions where the relationship between climatic forcing and human behavior remains to be demonstrated, the shift from the Late Upper Paleolithic and Mesolithic has been linked to and framed in terms of abrupt climatic changes occurring between the Late Glacial and the Holocene. In response to abrupt climatic forcing starting around the Late Glacial Maximum and followed by climatic events such as the Bolling–Allerød and the Younger Dryas in the Terminal Pleistocene, archaeological data pertaining to cultural and behavioral shifts of hunter-gatherers have been explored on a regional and pan-regional scale (Crombé et al., 2011; Donahue and Lovis, 2006; Huntley et al., 2013; Lovis et al., 2006). Within the
framework of the INQUA Project 1404, this study presents an overview of our current knowledge of economic activities among foragers from the Late Upper Paleolithic and Mesolithic cultures in the southern steppe of Eastern Europe.

The paper considers the period from the Late Glacial Maximum (Greenland Stadial 2b: 19-18,500 uncal 14C BP) over the Bølling–Allerød interstadial (Greenland Interstadial 1: 12,500-11,000 uncal 14C BP), Younger Dryas (Greenland Stadial 1, 11,000-10,000 uncal 14C BP) and up until the Holocene warming ~6000 uncal 14C BP. This interval is characterized by relatively abrupt climatic changes that preceded the beginning of the Holo-
cene as well as the climatic amelioration, which followed thereafter (Birks and Ammann, 2000; Brooks and Birks, 2001; Davis et al., 2003). The Greenland ice core records indicate that climatic fluctua-
tion was marked globally and led to large environmental shifts on a local scale, triggered by the decrease in sea level, increased humidity and temperature, as well as changes in the floral and faunal communities (Burke et al., 2014; Clark et al., 2012; Rosen et al., 2014; Thiagarajan et al., 2014; Yanko-Hombach, 2007). This instability drove Upper Paleolithic foragers to adapt to their changing environment, which is associated with the rise of the Mesolithic cultures.

Regions with a long history of hunter-gatherer occupations are often characterized by the abundance of karst systems, which resulted in comparatively good preservation and visibility. How-
ever, Eastern Europe has provided key archaeological records of human settlements and movement across open landscapes (Hofecker, 2002). Thus, archaeological investigations of open air settlements have the potential to address the broader spectrum of hunter-gatherer adaptations and can complement our under-
standing of hunter-gatherer behaviors that is often biased towards cave and rockshelter sites. Drawing on this interest, we consider open air sites in the Late Upper Paleolithic and Mesolithic sites from the southern steppe of Eastern Europe.

This paper constitutes a review article based on a combination of original unpublished data from recently studied/revised collection and a summary of literature and new studies, which entail cultural and faunal data with ge-referenced localization and radiometric dates of the archaeological sites. Current data indicate that hunter-gatherers in the Late Upper Paleolithic continued to exploit large ungulates for subsistence, a pattern that deviated little over most of the Late Paleolithic period. Changes, when observed, reflect shifts in the commonly targeted species by hunters. Bison and horses are the most dominant fauna in the southern steppe, depending on the region and the time interval. In contrast, the Mesolithic record shows greater diversification in the choice of large game prey as well as greater emphasis on gathering/fishing practices, and as a whole reflects a shift to a more regionally vari-
able diet.

2. Southern steppe of Eastern Europe

The current biome in Northwestern Eurasia consists of a mix of tundra, taiga, forest and steppe. Steppes stretch geographically from the lowlands of Inner Mongolia to the west coast of the Black Sea and parts of Hungary. It is one of the biologically and culturally rich environments that is threatened today by human impacts and has been the subject of multidisciplinary conservation efforts (Antonchikov et al., 2002; Korotchenko and Peregryn, 2012). It has been postulated that patches of relict from the Quaternary steppe exist today in Eastern and Western Beringia and the Altai-Sayan Mountains of Central Asia (Kienast, 2007; Pavelková Ričánková et al., 2014).

The past distribution of the steppe biome, which emerged roughly two million years ago, was larger than the present, as it originally covered most of mid-to-high latitude Eurasia, but the spatial diversity and temporal evolution of the prehistoric biome continue to intrigue paleoecologists and archaeologists alike. According to paleoenvironmental reconstructions, the steppe of the Pleistocene was locally heterogeneous, yet homogeneous on the continental scale (Pavelková Ričánková et al., 2014).

The tundra steppe is one of the most known biomes of the past, an ecological system that has received considerable interest in Quaternary research (Bigelow et al., 2003; Edwards and Armbuster, 1989; Guthrie, 1990; Hibbert, 1982; Kahlke, 1999; Kozevnikov and Ukraintseva, 1999; Yurtsev, 2001; Zimov et al., 2012). Environmental conditions from middle to higher latitudes in the Pleistocene were characterized by a cold and dry continental climate (Kienast, 2007). However, we have yet to fully understand the past biome of Eastern Europe in the Pleistocene due to several issues, including the lack of systematic sampling of paleoenviron-
mental record with chronological depth, creating geographical biases, as well as the resolution of the paleoenvironmental records, which allows us to correlate multiple sampled sites for regional-scale data (but see Haesaerts et al., 2010).

The tundra and steppe vegetation is indicative of the diversity of the plant communities in northern Eurasia and attests to the exis-
tence of several zonal biomes that were interstratified in the zone (Kozevnikov and Ukraintseva, 1999). The vegetation is largely dominated by herbs including tufted grasses, sedges and dwarf shrubs, which are found in the steppes of middle to high latitudes and in the Arctic tundra today (Elias and Crocker, 2008). Furthermore, the extreme seasonal fluctuation of moisture is documented by grasses typically linked to meadows as well as littoral plants that inhabit the shores of small lakes with unstable water levels (Kienast, 2007).

The tundra steppe has also been linked to a faunal community with no modern analogs. A notable feature is the large biomass of grazing animals, epitomized by extinct woolly mammoths and woolly rhinoceroses, hence the term ‘mammoth steppe’ (Guthrie, 1982, 1990; Kahlke, 2014). Many East European sites are known for the rich presence of mammoth remains exploited for dietary needs and their use as raw material for artifacts and structures. One of the known examples of Paleolithic dwelling structure was con-
structed from cranial and post-cranial remains of mammoths at sites such as Mezin, Molodova I, Gontsy and Mezhyrich (Demay et al., 2012; Iakovleva et al., 2012; Peán, 2015; Pidoplichko, 1998; Soffer, 1985). However, while taphonomic and sampling biases must be taken into account, zooarchaeological and paleontological records show that the density of mammoth population varied across the steppic landscape in Eastern Europe (Ponomarev et al., 2013; Puzachenko and Markova, 2014; Velichko and Zelikson, 2005). Megafauna (woolly rhinoceros and woolly mammoth) are particularly scarce in the area that some have referred to as the southern steppe (or the Black Sea steppe) in the Final Pleistocene (Anthony, 2007).

In the present, the region between the north of the Black Sea and ~48°N is characterized by the Pontic steppe (Korotchenko and Peregryn, 2012). The southern steppe of Eastern Europe extended eastwards from the Danube river and in the northern area of the North Sea below 48°N, traversing the Volga Valley and reaching Kazakhstan. Beginning at 32,000 uncal 14C BP, the Black Sea under-went the last phase of regression, and the sea level reached 110 m below the present at LGM (Bahr et al., 2008; Shmuratko, 2007). Additionally, the change in the sea level led to the forma-
tion of a lake in the place of the current Black Sea while the Azov Sea was fully part of the continent, and the Crimea was geographically part of the rest of the landmass, making up the southwestern margin of Eastern Europe (Winguth et al., 2000). The transgression of the Black Sea occurred beginning at the Belling-
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