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New estimations of habitable land area and human population size at the Last Glacial Maximum

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ABSTRACT

The estimation of human population size during the Pleistocene is complex, and one which has been dealt with extensively in the literature. However, because many of these previous estimations are based in part on archaeological site distributions, they are more a reflection of present-day geography than of what the Earth looked like in the past. We address this issue by calculating an estimation of habitable land area during the Last Glacial Maximum (between 22 and 19 kya) when sea level was 120 m lower than today using the polygon creation function in Google Earth. We then subtract areas of land that were likely uninhabitable during the LGM — either due to glacier cover, extreme aridity, elevation, or areas at high latitudes. From this, the combined habitable land areas of Eurasia, Africa and the Australian land-mass are estimated as 76,959,712.4 km^2. This estimation is then coupled with population density data for medium-to large-bodied carnivores, and ethnographic population density data for hunter—gatherers culled from the literature. Total human census population size in the Old World during the Last Glacial Maximum is estimated at 2,117,000—2,955,000 based on carnivore densities and 3,046,000—8,307,000 for hunter—gatherer densities.

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1. Introduction

Prehistoric human population size is a fundamentally important question in paleoanthropology. Evolutionarily speaking, it is populations that evolve, and since smaller populations are more likely to go extinct than larger ones, population size is a critically important variable in evolutionary biology (Harmon and Braude, 2010). With regard to human evolution, population size and density played a role in the origins and spread of modern human behavior (Powell et al., 2009; Stringer, 2012), and it is a central question in the debate over the geographic origins and early migrations of anatomically modern humans. One of the strongest arguments against the multiregional hypothesis for the evolution of modern humans is that it requires a large enough population size at any given time to have maintained gene flow across the Old World (Holliday et al., 2014).

Issues such as effective population size versus census population size of Pleistocene human populations are used by proponents of both the Recent African Origin [RAO] and Multiregional Evolution [MRE] models of modern human origins (Eller et al., 2009; Ray et al., 2005; Rogers and Harpending, 1992; Wolpoff et al., 2000). Effective population size (N_e), originally defined by Sewall Wright (1931), refers to the breeding population, including both males and females, of a species. N_e is a subset of individuals within the census population number (N). The relationship between N_e and N is a complicated one that can be affected by habitat variables as well as population expansion and contraction, and recent studies have indicated that there is likely no simple relationship between the two (Belmar-Lucero et al., 2012; Palstra and Fraser, 2012). These concepts play an integral role in any discussion of the origin and spread of modern humans, and N/N_e estimates have been used to support sometimes contradictory models. For example, a small N_e size during the Pleistocene has been cited as evidence against MRE, as it would have been unlikely that the sufficient level of gene flow MRE requires could have been maintained across the Old World with so few humans spread over such a large area (Harpending et al., 1993, 1998). Supporters of MRE have responded that population expansions and contractions, along with local population extinction, were the mechanism of gene flow during the Pleistocene, preventing regional speciation events (Eller et al., 2009).

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The issue of effective and census population size is significant from the perspective of gene flow, and also similarly in questions of the transmission of culture. In his book *The Selfish Gene*, Richard Dawkins (1976) first popularized the concept of units of human culture ("memes") being analogous to the role genes play in Darwinian evolution, and over the past 30 years, using an evolutionary framework to explain the evolution of human culture has drawn much attention from social scientists (Atran, 2001; Bentley et al., 2004; Cavalli-Sforza and Feldman, 1981; Eerkens and Lipo, 2005; Henrich, 2001; Mesoudi et al., 2004; Shennan, 2000). If early human culture may be considered as an inheritance system of adaptive information (Shennan, 2002), population size and density play as important a role in the evolution of culture as they do in the strictly biological processes involved in the evolution and spread of anatomically modern humans. Dual inheritance theory postulates that culture and genes have coevolved in modern humans by natural selection, and operate in similar ways (Richerson and Boyd, 1978). Selection operates on variation, both genetic and memetic, and variation is increased as population size and density are increased. Cultural transmission of ideas can occur more quickly, and new information can be better retained, in a large population (Eerkens and Lipo, 2005). Therefore, estimations of Pleistocene population size are important and integral to a wide range of paleoanthropological debates.

These issues have been covered in great detail in the literature, but the glaring omission, however, is that to date, very little attention has been paid to calculating population densities and population size based on actual land area estimates, and in particular land area estimates that take into account the lower sea levels associated with glacial periods. Without accurate Pleistocene habitable land area estimates, population density and size estimates will simply not be reliable.

The estimation of prehistoric population size is likewise problematic in numerous ways. In the past, researchers have relied on archaeological site distributions and/or estimations of hunter-gatherer population densities to estimate population size (Hassan, 1981; Binford, 2001; Bocquet-Appel et al., 2005). The "dates as data" method for regions around the world, championed thirty-five years ago by Rick (1987) and many others since (Holdaway and Porch, 1995; Kuzmin and Keates, 2005; Peros et al., 2010; Shennan and Edinborough, 2007), relies on the complex relationship between chronometric dates and human occupation of a given region. The number of dates is directly related to the extent and frequency of occupation, and thus represents human activity at that moment in time (Rick, 1987). These data may theoretically be used to make inferences about migration and settlement patterns, demography, and population density.

While this method has experienced a surge in popularity in the past thirty-five years, it is not without limitations. Surovell and Brantingham (2007) argue that this method does not highlight demographic trends, but rather taphonomic bias. Taphonomic processes such as the weathering and erosion of older material lead to an overrepresentation of more recent material. Therefore, any reconstruction of prehistoric populations through time will suggest relatively more activity in a given region in recent times than in the more distant past, whether that is an accurate reflection of the record or not (Surovell and Brantingham, 2007; Surovell et al., 2009). Williams (2012) highlights other methodological problems including the issue of inadequate sample sizes, sampling errors resulting in skewed results, and the influence of radiocarbon calibration on analyses.

This approach also carries with it several problems we wish to address more specifically with the current study. First, there were likely areas of occupation that left no archaeological record, the significance of which is only just now being recognized (Bailey and Flemming, 2008; Bicho and Haws, 2008). Second, large potentially habitable land areas that were exposed during glacial maxima are largely unavailable for study due to Holocene sea level increases. Evidence indicates that the exploitation of marine resources likely played a significant role in the population and geographic expansion of anatomically modern humans after 150 kya (Erlandson, 2001). Additionally, the early colonization of Australia by 50 kya (Thorne et al., 1999) is suggestive of a seafaring ability and implies regular exploitation of marine resources (Allen and O'Connell, 2008). Theoretical biases in modern archaeology have led to an underestimation of the importance of marine resources and coastal environments during the Middle and Upper Paleolithic. These biases are based on the relative rarity of coastal Pleistocene archaeological sites in Europe, which was interpreted by archaeologists in the late 20th century as evidence that humans did not regularly exploit marine resources until Early Holocene (Bicho and Haws, 2008). However, if these coastal areas were occupied during glacial maxima, there would be a clear bias in the archaeological record, as those sites would have been submerged when sea level rose. Those now-submerged coastal regions would potentially have been more productive during glacial periods than arid inland landscapes, and thus more attractive as settlement locations (Bailey and Flemming, 2008). By ignoring these now-submerged areas, we would ignore some of the most logical areas of human occupation during glacial periods. Third, it is likely that many Pleistocene humans lacked the technological sophistication to live at population densities comparable to those of hunter-gatherers in the ethnographic present (Churchill, 2014; Marlowe, 2005; Richerson et al., 2009). Population size and density are inextricably linked in the archaeological record. Increased population density requires technological innovation to more efficiently extract adequate resources from the environment, and the maintenance of that technological innovation requires a certain level of population density. Neither of these conditions likely applied to most Pleistocene groups, as they lacked both technological sophistication and high population density. Therefore, Pleistocene human population sizes based on hunter-gatherer data from the ethnohistoric present are almost certainly gross overestimates, at least prior to the Upper Paleolithic (Holliday et al., 2014).

In order to address these issues, we present a new method for estimating habitable land area during the Last Glacial Maximum (LGM). The period known as the Last Glacial Maximum began when global ice volumes reached their maximum between 22 and 19 kya (Clark et al., 2009; Yokoyama et al., 2000). These ice volumes remained fairly constant through 19,000 years ago, when the climate began to warm and sea level began to rise. The method and data we present include areas that were exposed during glacial maxima but are below current sea level. We estimated the areas of Eurasia, Africa and Australia when sea level was 120 m lower using the polygon creation function in Google Earth, which calculates the area within the polygon. We couple these data with population density data for wide-ranging medium-to large-sized carnivores and recent human foragers to estimate Pleistocene population size.

2. Material and methods

2.1. Land area estimation

We previously used this method to calculate habitable land area in Africa and Eurasia proper during glacial maxima (Gautney and Holliday, 2013; Holliday et al., 2014). We reported estimates of Eurasia and Africa when sea level was at its highest during the LGM using the polygon creation function in Google Earth. This function calculates the land area contained within the polygon. Google Earth is a free geographical information and virtual map program