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Modeling the role of fire and cooking in the competitive exclusion of Neanderthals

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A B S T R A C T

The Neanderthal body was more robust and energetically costly than the bodies of anatomically modern humans (AMH). Different metabolic budgets between competing populations of Neanderthals and AMH may have been a factor in the varied ranges of behavior and timelines for Neanderthal extinction that we see in the Paleolithic archaeological record. This paper uses an adaptation of the Lotka–Volterra model to determine whether metabolic differences alone could have accounted for Neanderthal extinction. In addition, we use a modeling approach to investigate Neanderthal fire use, evidence for which is much debated and is variable throughout different climatic phases of the Middle Paleolithic. The increased caloric yield from a cooked versus a raw diet may have played an important role in population competition between Neanderthals and AMH. We arrive at two key conclusions. First, given differences in metabolic budget between Neanderthals and AMH and their dependence on similar or overlapping food resources, Neanderthal extinction is likely inevitable over the long term. Second, the rate of Neanderthal extinction increases as the frequency of AMH fire use increases. Results highlight the importance of understanding the variable behaviors at play on a regional scale in order to understand global Neanderthal extinction. We also emphasize the importance of understanding the role of fire use in the Middle to Upper Paleolithic transition.

1. Introduction

There is little academic consensus for the biological, cultural, and environmental factors behind the process of Neanderthal decline in Europe and the disappearance of this population from the archaeological record between 41,030-39,260 calibrated years BP (Banks et al., 2008a; Higham et al., 2014; Gilpin et al., 2016). An increasing range of evidence for flexible subsistence behaviors and ecogeographically varied diet breadth among Neanderthals (Barton, 2000; Madella et al., 2002; Adán et al., 2009; Cortés-Sánchez et al., 2011; El Zaatari et al., 2011; Lloveras et al., 2011; Hardy et al., 2013; Blasco et al., 2014; Henry et al., 2014; Sistiaga et al., 2014; Hardy and Moncel, 2011) challenges previous suggestions that dietary rigidity may have put the Neanderthal population at an adaptive disadvantage relative to anatomically modern humans (AMH). If differences in foraging adaptability cannot adequately explain a competitive disadvantage for Neanderthals, other factors must be considered as components of Neanderthal population decline.

Previous studies directly comparing physiology, behavior, and demography of Neanderthals and AMH (e.g., Stiner, 2001; Lieberman et al., 2009) have broadened our understanding of factors that could have influenced the shift from Neanderthal to AMH occupation of Europe. In this article, we use a multi-step mathematical modeling approach to test metabolic rates and energetics as a proxy for successful reproduction and the reduction of interbirth intervals. Previous applications of demographic modeling to archaeology (e.g., Zubrow, 1989; Lycett and Norton, 2010; Lycett and Eren, 2013; Gilpin et al., 2016) have provided a means of "watching" possible iterations of population interactions in a way that feeds directly back into interpretations of the archaeological record.

We adapt the Lotka–Volterra equations and persistence of predators model (Dubey and Upadhyay, 2004; Alebraheem and Abu-Hasan, 2012). This adaptation simulates relationships between the most important features of Neanderthal and human populations competing for the same food sources: the handling costs of foraging, differential Neanderthal and AMH metabolic

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rates, and death rates for both populations. A recently published study by Gilpin et al. (2016) applies a similar modeling approach to the competitive exclusion of Neanderthals by AMH as a result of differences in culture level. Their use of the Lotka–Volterra model and compelling results highlight the value in a modeling approach to studying ancient population dynamics. We aim to refine their cultural exclusion approach by applying a specific culture- and knowledge-based variable, the use and control of fire for cooking, as a quantifiable measure of the impact of cultural behavior on the persistence of two competing populations.

We first calculate the minimum raw meat energy requirements for test populations of Neanderthals and AMH to determine the initial metabolic advantage for AMH without fire use. We then model the same populations within the same parameters, but with a varying factor of fire use. We assume here that a decrease in digestion costs and the equivalent increase in caloric returns of prey correlate with reproductive success, in keeping with behavioral ecology principles for foraging (Stephens and Krebs, 1986). Modeling variable fire use produces discrete scenarios of rates of competitive exclusion that can be tested against the archaeological record in order to increase the resolution of our understanding of subsistence behavior during the Middle and Upper Paleolithic.

2. Neanderthal and AMH diets

Archaeological evidence from Middle and Upper Paleolithic sites in western Europe suggests that AMH tended to exploit a wider variety of food resources than Neanderthals (Drucker and Bocherens, 2004; Bocherens et al., 2014). Recent studies have highlighted instances of Neanderthal use of plant resources (Fiorenza et al., 2011; Hardy et al., 2012; Buck and Stringer, 2014; Henry et al., 2014) and small terrestrial prey animals (Hardy et al., 2013; Blasco et al., 2014), but this evidence is scarce in comparison to the evidence for use of these same resources by AMH. El Zaatari et al. (2016) suggest that whereas Neanderthals altered their diets in response to changes in climate and ecology, AMH were less affected by changes in vegetation and climatic conditions, but rather maintained broad hunting and foraging strategies that shifted along with changing technological complexes.

Analyses of nitrogen isotope ratios from Neanderthal and AMH specimens generally support the notion that Neanderthals typically focused on large terrestrial herbivores (Bocherens et al., 2005; but see Fiorenza et al., 2015). Isotope signatures from Neanderthal specimens tend to point to Neanderthals as top predators in their environments, with similar carbon and nitrogen isotopic abundances as other local carnivores (Drucker and Bocherens, 2004; Bocherens et al., 2005; Richards et al., 2008). However, neither the Neanderthal nor the AMH diet should be categorized as static. Both populations likely varied their hunting and foraging behavior to some extent based on local ecological conditions. Thus, to reduce variability in constructing this model, we assume challenging ecological conditions, such as those of glacial phases in western Europe. These conditions would have limited access to plant resources, and large herbivores would have been accessible, or even abundant, on the landscape.

3. Evidence for fire in the Paleolithic of southwest France

We focus on southwest France, an area for which there is a rich and well-studied Paleolithic record, but which lacks a deep record of published evidence for fire use. Roebroeks and Villa (2011) conducted a survey of publications citing evidence for fire throughout Paleolithic Europe. Of these, eight were located in southwest France (Roebroeks and Villa, 2011: Dataset S1) and were dated between MIS 5 (approximately 130,000-80,000 years BP) and MIS 3 (approximately 60,000-25,000 years BP), predominantly associated with the Middle Paleolithic. To these we can add two sites: Abri Pataud, where evidence for combustion features exist (Marquer et al., 2010), and more recent work at La Ferrassie (Turq et al., 2014), which identified combustion features as well.

This scarcity of evidence for fire use in the Middle Paleolithic may be a reflection of a number of factors. The composition and function of a fire varies depending on the needs, preferences and available resources of an individual or group (Bellomo, 1993; Sergant et al., 2006). It is therefore unrealistic to assume that these fires will leave an archaeological “signature,” (Aldeias et al., 2012; Backhouse and Johnson, 2007; Mallol et al., 2013) and that this signature will be recognizable. When evidence for fire is present, it may not be observed or reported, especially as excavation techniques may not include systematic sampling for fire use proxies. Taphonomic processes may also affect the overall frequency of visible sites per time period and region (Surovell and Brantingham, 2007; Surovell et al., 2009). Sandgathe et al. (2011b) suggest that a more meaningful approach to the frequency of fire use in the Paleolithic would be a review of the number of site occupations with good evidence for fire relative to the total number of site occupations known for a particular region and time period.

There is evidence for fire use by Neanderthals from multiple Middle Paleolithic sites in France (Gowlett, 2006; Sorensen et al., 2018; Rots et al., 2011; Sorensen et al., 2014; Rots, 2015; Sorensen and Claud, 2016; Heyes et al., 2016). In contrast to these data, however, Sandgathe et al. (2011a,b) point to the fact that when fire appears in the archaeological record of the Middle Paleolithic, it is seen only in a small percentage of sites in any given time period, and often only within a small percentage of layers within a site. This indicates that Neanderthals were unlikely to have been obligate users of fire and perhaps lacked the technological ability to produce fire (Dibble et al., 2017; Sandgathe and Dibble, 2017). However, some groups of Neanderthals were certainly knowledgeable about the properties of fire and used it as a tool for fire, light, cooking, and tool preparation (Henry et al., 2014; Brown et al., 2015; Blasco et al., 2016; Aranguren et al., 2018) and for heating pitch for hafting (Rots, 2011; Wragg Sykes, 2015; Schenck and Groom, 2018).

Regardless of whether Neanderthals were able to make fire or instead only maintained fire sourced from natural origins such as lightning strikes, adequate fuel for prolonged fire use may have been sparse in open glacial environments (Théry-Parisot, 2002; Henry, 2017). This environmental factor might explain why evidence for fire is much less prevalent in certain periods of the Middle Paleolithic (Goldberg et al., 2012). Neanderthals also may have been able to cope with colder temperatures without fire due to their more robust musculature (Steegmann et al., 2002; Froehle and Churchill, 2009). However, maintaining normal body temperature in cold temperatures would have been metabolically costly. In terms of evolutionary success, how might populations of fire-using Neanderthals fare when placed in competition with anatomically modern humans, who certainly possessed the ability to manufacture fire? This study aims to address the gaps in the archaeological record where evidence for fire use is scarce. Through mathematical modeling we aim to understand the extent to which the habitual use of fire potentially affected the adaptive fitness of Neanderthals and AMH.

3.1. Fire and cooking

Cooking, defined here as the use of heat to prepare food for consumption, is sometimes characterized as “a technological way of externalizing part of the digestive process” that “not only reduces toxins in food but also increases its digestibility” (Aiello and Wheeler, 1995, p. 210). These effects potentially represent significant amounts of metabolic energy that could be repurposed. A