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The effect of terrain on Neanderthal ecology in the Levant

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ABSTRACT

Our study assesses the influence of differences in terrain and locomotor energetics on the land-use strategies and settlement patterns of Levantine Neanderthals and Modern Human – Early Upper Paleolithic groups through a digital application of site catchment analysis. Our findings indicate that Neanderthals habitually commanded smaller site exploitation territories (SETs), principally situated in the rugged Mediterranean Woodlands of the Levant, whereas early Upper Paleolithic groups generally enjoyed larger SETs and displayed a more generalized, wider settlement range encompassing both rugged woodland and more regular, level steppe landscapes. The broader implications of these findings may explain the biogeographic limits on the Neanderthal dispersal into Southwest Asia.

1. Introduction

Variation in terrain is generally accepted as one of the fundamental factors in understanding ecological adaptation, even to the extent that the common names of many taxa are often reflective of their habitats as defined by terrain; e.g., mountain gazelle, upland and lowland gorillas and so forth. While terrain is recognized as an important variable in general ecologic research, paleoanthropologists have given little attention to the adaptive responses of hominins to variations in terrain or landscape features, and this is especially relative to Neanderthal ecology. The interrelationship of Neanderthals and their environment has been examined largely from the perspective of biotic evidence of floral and faunal remains and attendant climatic reconstructions. Given their inherent energetic and locomotor differences from modern humans, an understanding of the effect of terrain on Neanderthal foraging patterns is especially relevant as to how variations in landscape influenced Neanderthal land-use and settlement-procurement patterns and, in turn, their biogeography (Burke, 2006; Miller and Barton, 2008; Finlayson and Carrión, 2007; Uthmeier et al., 2008; Churchill, 2014).

Advances in satellite imagery and digital science have prompted a wide-range of researchers to use terrain measures as a means of better defining the biogeography of plant and animal populations and to correlate their distributions to other landscape features. In the research reported upon here, we adopted a similar strategy using satellite imagery and geo-spatial digital data to assess the degree to which variation in terrain influenced the behavioral ecology of Neanderthals within the Levantine Near East. At a more specific level, our approach involved site catchment analysis (Vita-Finzi and Higgs, 1970; Bailey and Davidson, 1983) as a means of integrating site specific, digital data and assessing the degree to which terrain may have played a role in shaping the foraging strategies of Neanderthals and in producing any regional adaptive differences between Neanderthals and Anatomically Modern Human (AMH) groups. In comparing the effects of terrain on Neanderthals and AMH groups, we focused on site-specific data associated with the latest proposed pulse of modern human expansion into the Levant from Africa and/or Arabia during MIS 4 – early MIS 3, reflected in early Upper Paleolithic (UP) sites.

2. Site catchment analysis

The underlying concept of site catchment analysis (SCA) is that prehistoric groups exploited resources habitually within a nearby site exploitation territory (SET) and occasionally from more distant sources within a site catchment (SC) conditioned by the competing factors of the economic value of resources and the energy expended in procuring them, essentially following the law of diminishing returns. The term site territory was initially used by Vita-Finzi and Higgs (1970), but Bailey and Davidson (1983) suggested the term site exploitation territory (SET) to avoid confusion with social, defended site territories. Bailey and Davidson (1983) also proposed that SCA and STA be distinguished, a suggestion not followed here

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in that we view a SC as a larger spatial scale that encompasses one, or perhaps, several site territories. In any event, this is a topic beyond the scope of our paper. In many ways, at a more detailed level, this notion parallels the fundamental ecological concepts of optimal foraging theory as expressed in equations including such specific variables as search time, energetic expenditures and food yields. In operationalizing SCA, researchers have adopted different approaches in determining the time-distance limits of a SET and the manner in which the configuration of a SET is reconstructed around a site. While it is given that there must be some finite spatial limit to the area about a site that was exploited, the question is, how is this to be determined? In their seminal study, Vita-Finzi and Higgs (1970) used ethnographic observations to establish time (2 h) and distance (10 km) limits in configuring their SETs, measures that most researchers have subsequently followed. Although the 2 h outbound time for foraging from a base-camp has been traditionally employed in site catchment studies, this likely represents the lower range of foraging time in that more comprehensive ethnographic data indicate a range of 2.5–9 h and a clear difference between average female (2.8 h) and male (5.9 h) foraging times (Binford, 2001, p. 235–38). In reconstructing a SET for a foraging group there are numerous variables such as ground conditions (sand, snow, rough landscapes, thick vegetation), carried load, and even social considerations that might affect forage time-distance, but topography and locomotor energetics are the most important factors, at least the ones that are reasonably knowable.

In practice, SCA was initially based on actualistic assessments of SETs by walking out from a site along a number of arbitrarily selected, 2-hour transects and then visually interpolating these distant points on a map (Higgs, 1975; Bailey and Davidson, 1983). Given the difficulty in conducting actualistic assessments of SETs in many archaeological projects, researchers have adopted another approach that simply involves overlaying a circle of 10 km radius on a map around a site. While this “magic circle” approach is quick and convenient, it fails to reflect the importance of terrain in regulating energetic expenditures and ultimately in spatially defining a SET. In recognizing the importance of terrain variations to SET reconstructions, Bailey and Davidson (1983) devised a technique based upon Naismith's Rule that calculated hiking time/distance in consideration of variation in elevation. Their technique allowed for a relatively precise reconstruction of a SET using the time-distance-elevation variables provided in the Naismith equation applied on a topographic map. In the research program described here, we generally follow the approach introduced by Bailey and Davidson (1983), but introduce a digitally-based methodology that is sensitive to variations in terrain as well as differences in hominin locomotor energetics.

A SET can be examined using two complimentary approaches. The first is the area (km^2) of a SET and the second is the Accessibility Index (AI) that compares this area to the area of a hypothetical SET around a site that displayed level, unvarying terrain. An AI, factoring in the differences in hominin energetics, is seen as a proxy of the ruggedness of a SET and its actual effect on the foraging limits of Neanderthals and modern humans. The AI is calculated for each site by comparing the actual SET based on topography to the SET area generated with no topography (a completely flat plain). This flat digital elevation model (DEM) functions as a ‘hypothetical maximum’ that can be walked within 2 h without any influence from topography. The AI is calculated by dividing the area of a SET conditioned by topography by the hypothetical maximum SET to demonstrate the influence of site specific topography. For example, a catchment with an AI of 0.70 would mean that 70% of a potential 100% of the SET area surrounding a site with unvarying terrain could be exploited within a 2 h walking time, based on specific hominin energetics. Coastal sites, especially those framed by very rugged inland terrain, often displayed exceptionally small SET areas and AI's because of their limited access to exploitable terrestrial landscape and in these cases the implied ruggedness of the AI is likely exaggerated. However, in such cases the SET area and AI nevertheless provide an actualistic representation of the foraging parameters for the prehistoric occupants of these shoreline sites.

3. Neanderthal locomotor energetics

When studying how Neanderthals related to their environment it is also important to keep in mind that Neanderthal locomotor energetics differed from those of modern humans. Looking at gross morphology, Neanderthals had much shorter lower limbs, both absolutely and also relative to the trunk height, than modern humans as well as higher brachial and crural indices (Weaver and Steudel Numbers, 2005) and were more heavily muscled. There has been a debate in the literature if the unique morphology of the Neanderthals reflects an adaptation to climate (Steegmann et al., 2002; Aiello and Wheeler, 2003; Churchill, 2006) or a difference in locomotor energetics and mobility efficiency (Steudel-Numbers and Tilkens, 2004; Hora and Sladek, 2014), such as one that focused on a close range hunting strategy over persistence hunting that involved endurance running (Bocherens et al., 1999, 2001, 2005; Richards et al., 2000, 2005; Raichlen et al., 2011). In addition, Neanderthal morphologies (as indicated by both the effective inter-membral index and the length of the Achilles tendon) may have actually conferred a locomotive advantage in a rugged landscape when compared to modern humans who would have had a selective advantage in open habitats where running long distances would have been beneficial (Higgins and Ruff, 2011).

Current data also suggests that Neanderthals had a higher daily energetic cost of foraging compared to Early Upper Paleolithic modern humans based on lower limb length, body mass and both (Frohehle and Churchill, 2009; Snodgrass and Leonard, 2009). The lower energy expenditure of AMH is thought to have conferred a selective demographic and reproductive advantage and to have played an important role in the competitive exclusion between the two species.

Our understanding of Neanderthal locomotor constraints and high energetic costs has prompted proposals that Neanderthal groups exploited smaller foraging ranges than those of modern humans (Verpoorte, 2006; Macdonald et al., 2009), however, these notions have been largely hypothetical. Similarly, it has been argued that Neanderthals were limited to 0.5–1 h to 3 h average walking time for the acquisition of stable food resources, compared to 2–10 h for AMH hunter gatherers (Uthmeier et al., 2008, p. 487). Hayden (2012, p. 13) has suggested that Neanderthals habitually exploited areas within 5 km of sites based upon procurement distances of lithic resources as reported by Féblot-Augustins (1997) for Middle Paleolithic occupations. Although some materials were acquired from greater distances, 60–98% of all artifacts were acquired from sources within 5 km of the sites (Féblot-Augustins, 1997, p.62). Uthmeier et al. (2008) estimated walking times of 2–3 h, with concomitant distances of 6–8 km, for dedicated forays to chert sources from the site of Kabazi V in the Crimea, but they also note that most daily foraging activities were likely to have involved smaller SETs restricted to 2 h, one-way walking times. These data are noteworthy, in that a 5 km radius for SETs is considerably smaller than the mean distances reported in ethnographic contexts by Binford (2001, p. 238) for six groups of 7.3 km (female) and 8.7 km (male), by Marlowe (2005, p. 63) for 8 groups of 9.5 km (female) and 14 km (male) and by Churchill (2014, p. 308) of 6–17 km (female) and 12–25 km (male).

However, most energetic studies (but see Frohehle and Churchill, 2009) have focused only on Western European

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