

Abstract

The aim of this thesis is to test paleoecological hypotheses pertaining to early hominin dispersal events. During the Lower Pleistocene, hominins dispersed from Africa into Eurasia via the Levantine corridor. One of the earliest sites which testify to this dispersal event is the site of 'Ubeidiya. Situated in the central Jordan Valley, the fossil bearing strata are constrained between ca. 1.6 - 1.2 Ma and exhibits a rich lithic and faunal assemblage which span over several distinct stratigraphic units.

Over the history of research, different hypotheses have been put forth in an attempt to explain patterns of hominin evolution and environment change. These may be grouped into habitat specific hypotheses and the Variability Selection (VS) hypothesis.

Habitat specific hypotheses emphasize adaptations that arise as a response to the selection demands of a specific habitat. The savanna hypothesis suggests that early hominins evolved since the Miocene as a response to the increased aridity and open savanna environments. According to this hypothesis, the progressive increase in aridity throughout the Pliocene and Early Pleistocene, was the main selective force for the major morphological (bipedalism, large brains) and behavior (tool making, meat eating) characteristics associated with more developed hominins.

The alternative Variability Selection (VS) hypothesis promotes the idea that hominin adaptation was more influenced by an increase in different types of environments in long temporal time scales. Thus, hominin adaptation is primarily geared towards novelty and the ability to adapt to a variety of environments, as opposed to a single habitat.

This thesis utilizes this conceptual framework developed to the Lower Pleistocene dispersal events. The large mammalian fauna of 'Ubeidiya was analyzed in order to reconstruct the paleoenvironment at the site and to test for patterns of persistence and change throughout the sequence. Specifically, this study focused on patterns of relative abundance and community structure and its correlation with environmental change. Seven 'pooled strata' were analyzed based on adequate sample size and included two 'pooled strata' from the Li cycle and five 'pooled strata' from the Fi cycle.

In order to address this issues, four detailed research question were formulated in this thesis:

1. What are the agents of accumulation of the large mammalian fauna of 'Ubeidiya (i.e., hominin primary or secondary access to carcasses, carnivore kill site or scavenging, fluvial transport or natural background fauna)?
2. Can persistence or change be discerned among the large mammalian community structure in 'Ubeidiya throughout the sequence?
3. Can the observed pattern be attributed to local environmental change (the alternative hypothesis) or to various taphonomic processes (taphonomic null hypotheses)?
4. What is the paleoecological milieu of the 'Ubeidiya assemblages? are they more similar to that of African biomes, European or Mediterranean ones?

Identification of ecological patterns in the temporal scale depends first and foremost on the removal of the potential taphonomic biases in the fossil assemblages (density mediated processes, weathering, fluvial transport, hominins or carnivores as primary agents of accumulation and post depositional ravaging by hyaenas).

This thesis uses spatial autocorrelation analysis in the temporal scale as an approach to this problem. Biodiversity data (the dependent variables) were correlated with taphonomic variables (the taphonomic independent variables) which formed the null hypotheses as well as with the environmental independent variable which formed the alternative hypothesis.

Methodology included identification of the large mammalian assemblage specimens to species and body elements. Quantification used Number of Identified Specimens (NISP) for all biodiversity calculations (the dependent variables). Taphonomic attributes included weathering, size and shape of specimen and recording of the location of surface marks i.e., cut-marks and carnivore gnaw-marks. A total of 12,098 specimens were analyzed in thesis of which 2582 (29%) were large terrestrial mammals assigned to strata.

Results suggests that the accumulation of the large terrestrial mammalian fauna is similar for most 'pooled strata'. 'Ubeidiya assemblages probably represent an amalgamation of several processes. Thus, the faunal assemblages represented kill or near kill sites of large carnivores. These sites where subsequently exposed to low level utilization by hominins. The remains were further scavenged and accumulated by bone crushing carnivores such as the spotted hyaena.

Cut-mark and gnaw mark distribution, the absence of bone marrow processing and body part distribution are more consistent with secondary access of hominins to carcasses at the site which possibly removed selected elements to be processed elsewhere. Body part distribution provide equivocal results, heavily modified by density mediated process and specifically, carnivore ravaging. Nonetheless, I cannot negate the possibility that some early access to carcass was practiced

at the site, but it was probably not the *modus operandi* at the site. It is important to stress that the overall low frequency of cut-marks and the high proportion of specimens with no modification suggests that the hominin involvement in the accumulation of the assemblages is minimal.

The large mammalian fauna of 'Ubeidiya includes a total of 33 species. Two distinct faunal units can be distinguished. The first faunal unit includes 'pooled strata' III 11-13 and III 20 from the Li cycle and is low in species richness. The second faunal unit includes the 'pooled strata' in the Fi cycle (II 23-25, III 21-22, II 26-27, II 36 and II 37). Although there is no change in faunal composition throughout the sequence, there is a change in faunal abundance that may be related to the slow trend of desiccation identified both in gross and micro geomorphology. Thus, the older 'pooled strata' (II 23-25, III 21-22 and II 26-27) are assigned to sub-faunal unit B1 and the younger 'pooled strata' (II 36 and II 37) may be assigned to a sub-faunal unit B2.

The main factor which affects the change in faunal composition (presence-absence and abundance) is local environmental change. This correlation reflects the difference between faunal unit A and B. Local environmental change nor stratigraphy cannot account for the difference between the faunal composition of the two sub-faunal units in the Fi cycle: B1 and B2. There is a weak affect of local environmental change on the relative frequency of taxa throughout the Fi cycle as well as a weak affect of carnivore ravaging. Biodiversity analyses suggests that evenness is highly affected by carnivore ravaging and is a reflection of the selectivity of carnivore, notably hyaenas.

Detailed analysis of individual taxa suggests that this may be related to the change in abundance of forest taxa. Forest taxa (*Capreolous* sp. and *Pseudodama* sp.) abundance is weakly affected of first order environmental changes (between the Li and Fi cycles). 'Pooled strata' with high proportions of forest taxa (III 20) reflect periods of greater humidity and thus, greater forest coverage. This is confounded by the taphonomic bias of carnivore ravaging. 'Pooled strata' with high proportions of forest taxa, III 20 and II 26-27, were subjected to higher intensities of carnivore ravaging. Within the Fi cycle, the change in relative frequency of forest taxa cannot be attributed statistically either to any of the taphonomic null hypotheses nor to the alternative hypothesis.

The sequence at 'Ubeidiya can be interpreted as a slow decrease in forest habitat and increase in open habitat. The main decrease can be related to first order environmental change between the Li and Fi cycle (i.e., between 'pooled strata' III 20 and II 23-25). Throughout the Fi cycle, there is only a weak affect of the environment and in general a period of stasis. The increase in cervid proportions in 'pooled stratum' II 26-27 is related to carnivore ravaging rather to the environment. Recent paleomagnetic studies have suggested that this period may have lasted as long as ca. 325 Ka.

The large mammalian fauna of 'Ubeidiya responds to the local environmental change present

throughout the sequence either by stasis or by a change in relative frequency only. This is consistent with the recurrent assemblages model and emphasizes the ability of various species to withstand low and medium amplitudes of local environmental change over long time scales.

These results have important implications for paleoecological reconstructions. First, analysis of proportion of taxa is not only a reflection of the habitat but also of the intensity of the carnivore ravaging during this time period. This reduced the fidelity of our paleoecological reconstruction. Thus, 'pooled strata' with a high proportion of small-medium cervids may be erroneously interpreted to represent an environment of dense forest where in fact, the environment is actually more open but the assemblage was subjected to a high intensity of carnivore ravaging. Second, in regions of medium latitudes, where climatic change is often of medium and low magnitude, specific taxa may not respond to a climatic shift. Thus, the appearance of stasis in the fossil record in these regions, does not necessarily reflect environment change.

The fauna at 'Ubeidiya includes a high proportion of taxa of African biogeographic origin. It has been suggested that the presence of these taxa are indicative of savanna type environment. Paleoecological reconstruction of the site suggests that all 'Ubeidiya 'pooled strata' have high affinities with other modern and Plio-Pleistocene Mediterranean sites. Both faunal units present at 'Ubeidiya (faunal unit A and B) reflect various gradients of the Mediterranean biome. Thus, the presence of taxa of African origin such as *Peleovis oldowayensis*, does not indicate the presence of an African type savanna.

The dispersal of early hominins to 'Ubeidiya during the Lower Pleistocene would have required coping with a novel Mediterranean environment and with the various gradients within it. Successful dispersal events would have required a pre-adaptation to a wide range of habitats as suggested by the variability hypothesis.

The novelty of the thesis is three fold: First, it presents an in-depth paleoecological analysis of a Lower Pleistocene site of 'Ubeidiya with ramifications to early hominin evolution. Second, it analyzes different modes of response of mammalian fauna to low amplitude climatic change, this not only has implications for understanding hominin dispersal events in the Lower Pleistocene but also reveals some inherent biases in paleoecological reconstructions in low and medium latitudes. Third, it presents a methodology to increase the fidelity of paleoecological analysis using spatial autocorrelation in the temporal scale.