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Molluscs in the Levantine Upper Palaeolithic: implications for modern human diets and subsistence behaviour

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Chapter 1 • Introduction

From the Late Pleistocene onwards, Early Upper Palaeolithic (EUP) *Homo sapiens* groups (e.g., Levantine Early Ahmarians) dispersed into Eurasia around 50–40 thousand years ago (kya) (e.g., Klein 2008; Hublin 2013). These groups generally consisted of small populations often dispersed over large territories. Contrary to earlier humans dispersing into Eurasia, e.g., Levantine Initial Upper Palaeolithic (IUP) groups, EUP human settlement is characterised by increasing site counts and occupation intensity which has been interpreted as a sign of increasing population density (Powell et al. 2009; Mellars and French 2011; but see Dogandžić and McPherron 2013; Vaesen et al. 2016) throughout Marine Isotope Stage (MIS) 3 [~57–29 kya; Lisiecki and Raymo (2005)]. Thus, it appears that EUP *Homo sapiens* were better adept to tackle the difficulties of dispersal and long-term survival in new habitats than their IUP forbearers. What were the underlying adaptations that made this possible? To start addressing this question, we need to improve our understanding of the timing of human dispersal events, the routes involved in these events, and the environmental conditions under which successful dispersal events occurred. Equally important is to investigate behavioural adaptations (e.g., technology, social interaction, and subsistence strategies) to shed light on some of the potential factors underpinning the success of these dispersals.

This thesis contributes to our understanding of early Upper Palaeolithic (including both Levantine IUP and EUP) adaptations through interdisciplinary research on materials from the archaeological site of Ksâr 'Akil, Lebanon. The choice of this site is based on several important factors. First, it has played a central role in the *Homo sapiens* dispersal debate because of its location in the Levantine Corridor on the edge of Europe (e.g., Bar-Yosef 1987; Mellars 2004). Second, Ksâr 'Akil is well known for its rich early Upper Palaeolithic deposits, including multilayered IUP and EUP/Early Ahmarian deposits that are associated with *Homo sapiens* fossils. The IUP and EUP of the Levant are key in the debate around Upper Palaeolithic human dispersals into Europe because both technocomplexes have been connected to *Homo sapiens* dispersal events based on similarities in lithic technologies between the Levant and Europe (e.g., Bar-Yosef 1998, 2007; Tostevin 2003; Mellars 2006; Kuhn and Zwyns 2014; Hublin 2015).

The IUP/Emirian in the Levant has been argued to be the source of the Bohunician in Central Europe and to represent the archaeological signature of a population dispersal (Svoboda and Bar-Yosef 2003; Tostevin 2003; Škrdlá 2013). Along the same lines, it has been argued that the appearance of the Proto-Aurignacian in Europe is connected to a dispersal of Early Ahmarian human groups into Europe (e.g., Belfer-Cohen and Goring-Morris 2003; Mellars 2006; Zilhao 2006; Le Brun-Ricalens et al. 2009; Tsanova et al. 2012). Ksâr 'Akil is one of the few sites in the Levant (in addition to Manot Cave, Israel, and Üçağızlı I Cave, Turkey) that contain deposits spanning these critical time periods associated with human remains.

1.1 The role of shellfish in Palaeolithic diets

Exploitation of shellfish and other aquatic resources in general is thought to have been important in early hominid encephalization (e.g., Brenna and Carlson 2014; Cunnane and Crawford 2014; Joordens et al. 2014; Kyriacou et al. 2016). Marine molluscs and other aquatic resources are rich in polyunsaturated (omega-6 and omega-3) fatty acids in the form of arachidonic acid (AA) and docosahexaenoic acid (DHA). These are important in human brain development, and some of them, especially DHA, are difficult to obtain from other sources (e.g., Kyriacou et al. 2014). Recent archaeological discoveries indicate that the exploitation of aquatic resources has a long history among various hominid species. The earliest current evidence for the exploitation of freshwater fish is at FwJj20 (Koobi Fora, Kenya), dating to approximately 1.95 million years ago (Braun et al. 2010) and associated with the Oldowan. *Homo erectus* individuals may have consumed freshwater molluscs from approximately ≥ 400 kya in Trinil (Java, Indonesia) (Joordens et al. 2014).

The exploitation of coastal habitats has also featured in hypotheses concerning the interaction between *Homo sapiens* groups during the Southern African Middle Stone Age (MSA) (e.g., Marean 2014, 2015). Marean's (2014) hypothesis is that consistent use of these coastal habitats gave rise to the need to defend these territories, which likely led to intergroup conflict. A similar scenario for lakeshore access has recently been proposed for early Holocene groups in the Turkana Basin (Lahr et al. 2016). Intergroup competition over shore access could also have stimulated intragroup cooperative behaviours and so-called hyperprosociality (*sensu* Richerson and Boyd 2008), which Marean (2015) sees as one of the trademarks of modern human uniqueness. This hypothesis assumes reliance on intertidal marine resources and a central role of the coastal zone in hunter-gatherer mobility. Evidence for MSA coastal exploitation dates

back to MIS 6 and 5 (roughly 190–125 kya and 125–80 kya, respectively) when several coastal South African sites show evidence for shellfish gathering (e.g. Klein et al. 2004; Avery et al. 2008; Jerardino and Marean 2010; Langejans et al. 2012; Clark and Kandel 2013; Kyriacou et al. 2015; Jerardino 2016).

Furthermore, intertidal marine molluscs may have served as fall-back resources to tap into in times of dietary stress (e.g., Meehan 1977; Waselkov 1987) because they are easily acquired predictable resources that are available year-round (e.g., Shackleton and van Andel 1986; Kyriacou et al. 2014; Marean 2014; Jerardino 2016). In the eastern Mediterranean, for example, intertidal marine molluscs were predominantly gathered in winter during both the Epipalaeolithic Capsian and Neolithic phases at the Haua Fteah (Libya), whereas seasonality data for terrestrial fauna indicate that hunting was practised mainly during the summer, leading Prendergast et al. (2016) to suggest that shellfish were dietary supplements at times of resource depression. In the Mediterranean region in general, marine shellfish were exploited during the Middle Palaeolithic by both *Homo sapiens* and *Homo neanderthalensis* from MIS 5 onwards (e.g., Emiliani et al. 1964; Klein and Scott 1986; Stiner 1999; Finlayson et al. 2006; 2008; Colonese et al. 2011; Cortés-Sánchez et al. 2011; Barker et al. 2012; Fa et al. 2016).

The predictable availability of inter-tidal molluscs in coastal habitats has further been argued to facilitate human dispersals along coastal routes (e.g., Stringer 2000; Finlayson 2005; Mellars 2006a). In unknown terrain, coastal habitats may have provided a predictable source of molluscs that can readily be exploited (e.g., Fa 2008). In other words, whereas hunting terrestrial fauna in novel surroundings might prove difficult, marine molluscs are generally abundantly available on intertidal rocky shores. However, Fa (2008) argues that the low tidal amplitude of the eastern Mediterranean shores, due to the reduced intertidal zonation, would have supported fewer edible littoral molluscs than for example the western Mediterranean shores. He argues that these coastal habitats would therefore have been depleted rapidly, which would have necessitated moving to new coastal patches, thus promoting hunter-gatherer mobility along this type of coast. Similarly, Mannino and Thomas (2002) suggest that in a rocky shore context, if large-scale human dispersals along coastal routes are the result of many small-scale dispersal events, and if subsistence practices relied substantially on exploiting coastal resources, localised over-exploitation and patch depletion would have resulted in increased (residential) mobility (*sensu* Binford 1981). Although availability of edible shellfish would in these scenarios influence human mobility and dispersals, short-term local over-exploitation would not necessarily be evident in the archaeological record, if humans were passing through

rapidly, and such episodes might not have had a long-term impact on mollusc communities (Fa 2008).

Finally, evidence of intensified use of coastal resources is often taken to be an indicator of reduced residential mobility and/or population pressure (e.g., Stiner 2001, 2009; Steele and Klein 2013; Marean 2014). Similarly, incorporation of shellfish into the diet and broader use of the carrying capacity of a site's catchment area would arguably allow support of a higher population density (e.g., Stiner 2001) or would sustain smaller groups for a longer time (e.g., Finlayson et al. 2006; Fa 2008; Prendergast et al. 2016).

Thus, the archaeological record suggests that aquatic resources played a role in hominid diets of great antiquity, though their contribution has been considered marginal for most of the Palaeolithic (e.g., Erlandson and Moss 2001; Colonese et al. 2011; Clark and Kandel 2013; Jerardino 2015). This is especially true when optimal foraging models are used, which primarily consider the caloric value and energy intake of foodstuffs (see also Stiner, 2001, 2010). However, shellfish are a rich source of many essential nutrients: next to the aforementioned AA and DHA fatty acids, they are also rich in vitamins D, B12, C, A, and E; as well as iron, folate, potassium, and calcium (e.g., Hockett and Haws 2003; Haws and Hockett 2004). Hockett and Haws (2003) suggest that broader and nutritionally rich diets are important because they increase hominid fitness and help to reduce child mortality and interbirth intervals. In turn, when minimum energy requirements are met (including those from other food sources), this could have allowed for the population increase in Europe thought to coincide with the start of the Upper Palaeolithic.

Against this background, the primary goals of the research programme were to (1) provide a new chronology for the IUP and EUP occupations of Ksâr 'Akil, and (2) to analyse selected faunal assemblages from Ksâr 'Akil with the aim of providing insights into subsistence strategies of Levantine early Upper Palaeolithic *Homo sapiens* and understanding the implications of their dietary choices for human nutrition, health, and population density. The following sections briefly present the theoretical background relevant to the Ksâr 'Akil project.

1.2 Theoretical framework

Many scholars have argued that at the onset of the Upper Palaeolithic, parts of Eurasia saw an increase in population density. This is based in part on the number of sites and

archaeological artefact densities, as well as calculations of effective population sizes from genetic data (e.g., Bocquet-Appel et al. 2000, 2013; Lahr and Foley 2003; Mellars and French 2011, 2013; French 2015). Others argue that the increase in population density was less extensive than has been proposed. For example, Dogandič and McPherron (2013) argue that the tenfold increase proposed by Mellars and French (2011) is an overestimation, as the numbers for several Upper Palaeolithic phases were collated and not all proxies used are independent (but see French 2015). Davies (2007) argues for small ephemeral initial *Homo sapiens* dispersals at the start of the European Aurignacian based on site distributions and density. What were the underlying factors that facilitated these dispersals? Did, for example, past human diet play a role, and how can zooarchaeological data contribute to answering these questions?

Fluctuations in prehistoric human population densities have been investigated from zooarchaeological data sets worldwide using optimal foraging theory (OFT) and diet breadth approaches (e.g., Stiner et al. 2000; 2012; Stiner 2001, 2010; Munro 2004; Lyman 2008; Clark and Kandel 2013). OFT, follows the economic principle of optimisation, i.e., the action of making the best or most effective use of a situation or resource (MacArthur and Pianka 1966). Translated in archaeological terms, OFT rests on the assumption that an organism or population always tries to optimize subsistence practices, generally in terms of the capture of energy. Following the diet breadth model, overall foraging time depends on two factors: (1) the time it takes to encounter a suitable prey, i.e., 'search time', and (2) the time it takes to capture and process the animal after it has been located, i.e., 'handling time' (Fig. 1.1). Diet breadth models are built on the presumption that, in ideal circumstances, a hunter will only exploit the most profitable prey. In this way, the hunter's decision is based on whether it is more profitable to go after the encountered prey or to keep searching for a higher-ranked species (e.g., Winterhalder 1987; Kaplan and Hill 1992). A (substantial) rise in human population density would require a higher return rate, which in turn would lead to diversification of the diet to cope with the population's increased energy (i.e., calorie) requirements. The inverse of Simpson's (1/D) index (Simpson 1949), an index of taxonomic dominance in faunal assemblages, is often used to assess dietary breadth and the optimality of subsistence practices (e.g., Stiner 2001; Dusseldorp 2010; Lyman 2013). Following these assumptions, an 'optimal' diet consists of a small number of high-ranked taxa exclusively. Inversely, an abundance of many different lower-ranked taxa (e.g., small-bodied taxa low in energy yield or fast-moving taxa high in capture cost) would be indicative of the need to capture whatever hunter-gatherers could get their hands on, which suggests dietary stress (e.g., Broughton and Grayson 1993; Kelly 1995; Bird and O'Connell 2006).

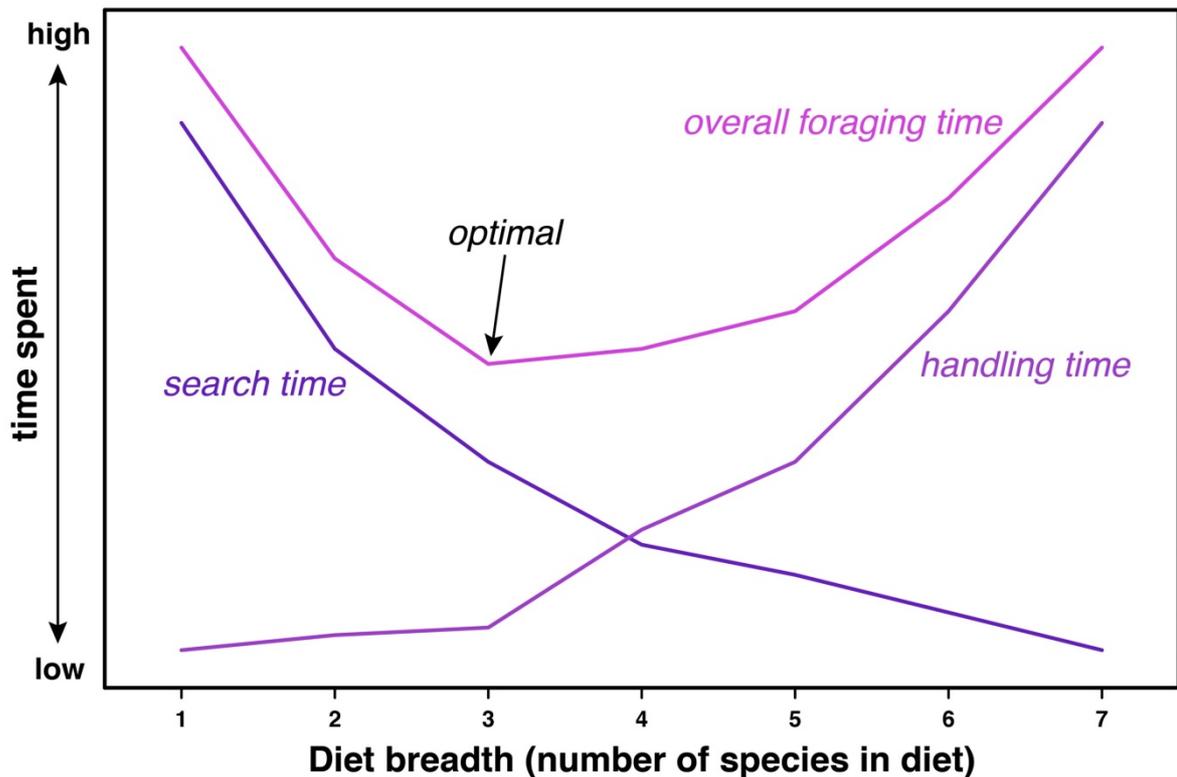


Figure 1.1: Diet breadth model.

Optimal foraging approaches have been criticised as too simplistic and not representing the full scope of hunter-gatherer subsistence behaviour that comprises more than just the optimal capture of energy (Smith 1983). However, these models have proven adequate to predict contemporary hunter-gatherer subsistence behaviour (see, e.g., Winterhalder 1987; MacArthur and Pianka 1966) and are likely equally useful when one seeks to understand the mechanisms and factors important in past hominid foraging behaviour (see also Dusseldorp 2009; 2010). In other words, OFT is a way of addressing subsistence data that can indicate if people are not foraging optimally from an economic perspective as well as if they are. Therefore, OFT forms a good starting point to understand the factors important in past foraging behaviour, including those that are not directly related to nutrition. Moreover, tools used in investigating optimal foraging—taxonomic dominance and evenness indices—have the additional benefit that they are useful for comparing patterns of animal exploitation between faunal assemblages through time at either a single site or between sites (see e.g., Lyman 2013). Based on these considerations, an optimal foraging approach is used to interpret the faunal data from Ksâr 'Akil.

Adding to the OFT debate, Hockett and Haws (2003) argue that it is not the capture of energy that should be optimized but rather the nutritional value of the diet (e.g., the intake of essential nutrients such as minerals, vitamins, and amino acids). Changing the 'currency' of the foraging model opens up a new area of exploration in human dietary studies. Using so-called nutritional ecology theory (NET), Hockett and Haws (2003; Haws and Hockett 2004) suggest that a broadening or diversification of the diet would result in a more varied and nutritious diet incorporating more essential nutrients. In turn, this would result in healthier populations with greater reproductive success (especially if they also invested in methods to decrease child mortality and interbirth intervals *sensu* Kaplan et al. 2000), ultimately contributing to population increase. Unlike in most OFT models, the decision to diversify the diet in a NET model is not necessarily a conscious one. In other words, even if a subsistence strategy is driven by non-dietary objectives (e.g., obtaining secondary products such as animal skins, tortoise carapaces for containers, mollusc shells for tools or ornaments, prey encountered on a search for other raw materials), the benefits of a varied diet will still affect the overall health of a population.

It is challenging to assess nutritional value of foods in past hunter-gatherer diets from the archaeological record, let alone to assess who ate what within the group. For example, organ meat is high in rare essential nutrients, but from bones remaining in a site, it is not always possible to discern if the organs were consumed in addition to the muscle and fat resources. Similarly, plant foods were likely a (substantial) part of Palaeolithic diets, but they are rarely adequately preserved at archaeological sites (Jones 2009; Henry et al. 2014). In contrast, shells generally preserve well archaeologically, and they constitute small food packages high in essential nutrients. Moreover, these essential nutrients need not be eaten in great quantities to have a positive effect on human health. Therefore, even the presence of low quantities of nutrient-rich foodstuffs—as they are often found at Palaeolithic sites—is informative about the dietary nutritional value. Thus, to assess dietary adaptations and their implications for early Upper Palaeolithic hunter-gatherers, I chose to focus on mollusc exploitation. To gain insight into the broader faunal-based subsistence practices, I complemented the results on mollusc exploitation with investigations of diet breadth and habitat exploitation of terrestrial fauna from the same archaeological context.

1.3 Thesis summary

This thesis investigates the subsistence behaviour of early Upper Palaeolithic (including IUP and EUP) *Homo sapiens* based on the remains of molluscs and terrestrial animals recovered from Ksâr 'Akil. A major aim in this respect is to gain insight into the timing and intensity of shellfish exploitation. I also aim to discuss the influence that dietary choices may have had for past hunter-gatherers in terms of health and development and whether these dietary adaptations could have influenced population density at the site, given the Upper Palaeolithic *Homo sapiens* dispersal events into Europe. More specifically, this thesis addresses the following research questions:

- (1) When were early Upper Palaeolithic foragers using the Ksâr 'Akil rockshelter?
- (2) What do both the mollusc and vertebrate faunas from Ksâr 'Akil tell us about how early UP foragers exploited those resources, in terms of selection and frequency?
- (3) What role does shellfish exploitation play in early Upper Palaeolithic subsistence practices?
- (4) Are there differences between IUP and EUP subsistence strategies, and if so, how may they be explained?
- (5) Are there general inferences from the Ksâr 'Akil case study for wider debates about landscape use, human health, demography, and their potential relationships to human dispersals?

To pursue these research questions, I conducted zooarchaeological investigations combining an OFT diet breadth approach with NET to evaluate subsistence practices and dietary adaptations of IUP and EUP groups. Specifically, I analysed shell assemblages to investigate mollusc use and consumption using a combination of zooarchaeological (including taphonomic), radiometric, and stable isotopic methods. The results are interpreted in the context of data from the vertebrate faunal assemblage, using a diet breadth approach to evaluate the exploitation of both sets of animal food resources.

In this thesis, I hold general conditions, such as geography, access to fresh water and raw materials, distance to the coast, and access to other habitats, as constant as possible by studying IUP and EUP assemblages from the single site of Ksâr 'Akil. As discussed above, this

site was chosen on the basis of several important factors. However, the excavations took place in the 1930s and 1940s, and the site is no longer accessible. Therefore, before any zooarchaeological study could commence, the integrity of the site, its chronology, and potential biases of the recovered faunal assemblages had to be evaluated. These issues, as well as the results of the various analyses, are presented in the following chapters.

Chapter 2 provides an overview of the Palaeolithic sites in the Antelias Valley in which Ksâr 'Akil is situated. This includes a summary of the various notes and interpretations of the rockshelter's stratigraphy and a brief account of the site's history of research, with a focus on faunal studies. It details the sampling rationale for the studied vertebrate assemblage and the cleaning and curation protocols. It also provides a basic account of the taphonomic signatures of the IUP and EUP assemblages studied and an overview of the faunal composition in terms of NISP (Number of Identified Specimens) and relative abundance. Data recording protocols for both the shell and bone assemblages and their rationale are provided in the Appendix A.

Chapter 3 discusses the site's chronology and implications of the age of specific Upper Palaeolithic technocomplexes and human fossils for understanding the timing and patterning of the Upper Palaeolithic human colonisation of Europe. A new chronology of Ksâr 'Akil is presented based on 16 AMS radiocarbon dates and Bayesian modelling. A thorough evaluation of sample integrity using three different independent data sets—amino acid racemization, geochemical characterization of all dated shells, and oxygen isotope analyses—is also discussed. At the start of this project, no direct dates were available on either IUP or EUP material, and the site's chronology was built on assumed ages that were in part extrapolated from dates from other parts of the sequence (Mellars and Tixier 1989). Because the Ksâr 'Akil stratigraphic sections are no longer available and because the materials we used for dating were excavated long ago (1937–1938 and 1947–1948), I and my collaborators developed novel ways using different lines of evidence to assess the site's chronology; we also invested substantial effort in detecting compromised samples. Detailed descriptions of the fresh approaches developed in the framework of this thesis are provided in Chapter 3.

While we conducted our study, Douka et al. (2013) published a chronology based on AMS radiocarbon dates on beach-collected shells from the same excavation campaigns that were potentially used for ornamental purposes. Our new data set of AMS radiocarbon dates on the live-collected *Phorcus turbinatus* molluscs that were consumed by Upper Palaeolithic humans provided significantly older (3000–4000 radiocarbon years) age estimations for both the IUP and

EUP deposits. Chapter 4 discusses discrepancies between our chronology and those of other scholars and proposes some steps towards resolving the remaining questions.

Chapter 5 evaluates the integrity of the mollusc assemblage as well as potential biases (e.g., post-depositional processes, excavation, and collection bias). This chapter also assesses the comparability of assemblages from different layers, excavation years, and recovery histories. Although there is in some instances evidence of extensive time averaging in the way that assemblages formed over a certain amount of time but appearing to be from a (semi) continuous event), there is no tangible evidence for the actual mixing of cultural material either post-depositionally or post-excavation. The mollusc assemblage is described in terms of taxonomic diversity and evenness, taphonomic signatures of different taxa and the ways in which humans used them (e.g., tools, ornaments, and food). The chapter especially focusses on the proportional use from a chronological perspective of both terrestrial and marine molluscs as a food resource relative to their exploitation as a raw material. Investigations include identification of anthropogenic modifications and determination of whether molluscs were gathered alive, which are prerequisites for demonstrating shellfish exploitation by humans. Finally, metric analysis of both live- and beach-collected taxa is used to highlight chronological trends in average mollusc size to investigate potential overharvesting of marine coastal resources (e.g., Mannino and Thomas 2002; Klein and Steele 2013).

Chapter 6 discusses the nature and timing of human shellfish gathering throughout the Upper Palaeolithic and explores how shellfish consumption would have affected hunter-gatherer diets. Seasonality of shellfish exploitation is investigated through the use of oxygen isotope analysis. These data help us better understand the role of this foodstuff throughout the year, and they provide indications on the timing of site occupation, past hunter-gatherer mobility, and overall landscape use. These data are substantiated with evidence from other faunal categories, such as avian, micro- and macro-vertebrate assemblages, that help us understand habitat diversity and human diet breadth. The emerging patterns gleaned from the data are compared with subsistence data from other eastern Mediterranean Palaeolithic sites. Finally, I discuss the implications of shellfish exploitation for past hominid diets in general from a NET perspective and highlight the differences between the IUP and EUP at Ksâr 'Akil.

Chapter 7 summarises the results of the previous chapters and presents a broad discussion of their implications for human subsistence strategies at Ksâr 'Akil. A particular focus is on the discussions on the role that shellfish played in past hunter-gatherer lifeways and on different

dietary adaptations of IUP versus EUP groups. The implications of these differences with regard to human health, life history, and dispersal events are explored.

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