Chapter 7

Palaeoecology: considering proximate and ultimate influences in human diets and environmental responses in the early Holocene Dnieper River region of Ukraine.

Malcolm C. Lillie and Sarah Elton

7.1 Introduction

Much has been written about the importance of palaeoecology and palaeoenvironments in shaping human evolutionary history. “Palaeoenvironment” is often used as a catch-all term that variously includes abiotic environmental elements such as those related to climate (e.g., rainfall and temperature), elevation, and the landscape (e.g., the presence of lakes and rivers, often reconstructed from sediment studies), and biotic components such as vegetation, invertebrates, and vertebrates. Climate, seasonality, and particular landscapes have all been invoked as selection pressures in early hominin evolution (e.g., DeMenocal, 1995; Foley, 1993; Winder et al., 2015). For modern humans, most often the focus of evolutionary medicine, there are clear examples of adaptations to their environments, such as genotypes that facilitate survival at high altitude (Beall, 2007). Palaeoecology is defined as the interaction of living organisms, including humans, with their environments, and is commonly considered alongside palaeoenvironmental reconstruction. Palaeoecology provides a wealth of examples of selective pressures within all periods of human evolution, including the roles of parasites, bacteria, viruses and other pathogens in disease causation and subsequent adaptation (see Chapters 8, 9, 10, 11, and 17). Consideration of diet is also central to understanding palaeoecology. A great deal of attention has been paid to the role of diet in human evolution (Chapter 5), from its influences on brain evolution and digestive tract morphology (Aiello and Wheeler, 1995), to discussions of the role that “Stone Age diets” play in contemporary human health (Eaton and Konner, 1985; Eaton and Eaton, 1999; Eaton et al., 1999; Cordain et al., 2000).

Palaeoecology and palaeoenvironments provide the context for evolution and the selective pressures that shape it. In formulating relevant hypotheses, it can be challenging to accommodate the immense temporal and spatial variation that humans have experienced over the course of our evolution (Elton, 2008). Indeed, some prominent and well-established narratives of human adaptation within evolutionary medicine (such as the “Stone Age diet”) tend to underplay the variation and diversity inherent in human populations in favour of perspectives that stress “mismatch” between the modern condition and a largely homogeneous past (Eaton and Konner, 1985; Eaton and Eaton, 1999; Eaton et al., 1999; Cordain et al., 2000). We argue that human evolutionary history is characterised by the exploitation of diverse habitats, consumption of diverse diets, and adoption of varied cultural and behavioural practices, a view that has been discussed elsewhere in the evolutionary medicine literature (Elton, 2008; Foley, 1995; Gowlett, 2003; Turner and Thompson, 2013, 2014; Ulijaszek et al., 2012). It is within this framework of palaeoenvironmental and palaeoecological diversity that we must consider the evolution of health and disease.

In this chapter, we bring together bioarchaeological data and evolutionary theory to give an overview of early Holocene human palaeoecology in changing environments. Given the immense temporal and spatial variation in environments across the globe, and across time, we necessarily focus on archaeological sites from one region and a restricted time-period, Mesolithic and early Neolithic assemblages from contemporary Ukraine. To date, central and eastern Europe has not been studied extensively in the context of evolutionary ecology and medicine, yet its archaeological record provides an ideal chance to examine detailed trends in diet and skeletal pathology in ecological and environmental context. Globally, it is clear that environmental diversity resulted in an equally diverse range of cultural adaptations and behavioural responses as human groups adapted their food procurement strategies. In turn, this may be reflected in biological variation in both space and time. Variability and fluctuations in the environment, ecology, prey species, plant biomass, and aquatic resources, combine to ensure that multidisciplinary approaches, open to the concept of variation, are required if we are to develop realistic and reliable interpretations of human responses in these changing and changeable palaeoenvironments. Study of the human skeleton offers the perfect opportunity to investigate biological responses to that variability and fluctuation in past populations, with stable isotope and palaeopathological analysis giving a window into the diets and health statuses of individuals and populations. Thus, using palaeopathological and isotopic studies of Ukrainian prehistoric populations, we examine dietary variation and health status in the context of Holocene warming and cooling, and discuss the impact that these might have had on cultural developments across the Mesolithic and Neolithic in Ukraine. We further use our case study of Ukraine to consider the relative importance of ultimate (evolutionary) and proximate (immediate) effects in determining the health of individuals and populations during the early Holocene "transition" period.

7.1.1 Background

The Holocene (the current geological epoch, which began ~12,000 years ago) is seen as a time of transition in many parts of the world from hunter-gathering mobile ways of life to a more sedentary and agriculture-based existence. Human populations in the earliest Holocene (referred to by archaeologists as the Mesolithic period) are, like those earlier in the Palaeolithic, generally characterised by mobile hunting and gathering (or combinations of hunting, fishing, and foraging strategies) (e.g., Zilhão et al., 2020). Somewhat later, in the Neolithic, it is commonly understood that many groups became more sedentary, with the adoption of agriculture becoming widespread. In the evolutionary medicine literature, much has been made of the transition to farming and its implications for human diet and health (Eaton and Konner, 1985; Eaton and Eaton, 1999; Eaton et al., 1999; Cordain et al., 2000), although some authors have drawn attention to the lack of a "revolutionary" transition or argued that the relatively recent Industrial Revolution may have had more profound impacts (Elton, 2008, 2016; Strassman and Dunbar, 1999). The bioarchaeological literature documents a decline in health with the transition to farming, also known as the first epidemiological transition (e.g., Cohen and Armelagos, 1984; Cohen and Crane-Kramer, 2007; Roberts, 2015).

Significantly, though, numerous studies have shown considerable overlap between foraging and farming at the Mesolithic-Neolithic boundary throughout central and eastern Europe. Despite the generalisation that Mesolithic equals hunting and gathering and Neolithic equals farming, Dennell (1983:15) stated that "...much confusion has arisen over how to distinguish food-extraction from food-production", and in some areas this remains a valid observation. There is increasing awareness that the key features of what we now recognise as farming — sedentary life, decreased mobility, food storage, domestication of plants and animals — have a prehistory that extends much further back than was originally assumed, into the very earliest Holocene and even the Palaeolithic (e.g., Boaretto et al., 2009; Brown et al., 2009; Dobney and Larson, 2006; Revedin et al., 2010; Wu et al., 2012), and that there was no single point at which these behaviours were adopted in combination across the world. To this day, there exists in some regions a lack of a clear dichotomy between modern hunting and farming groups, which is not simply due to biases in research strategies or a lack of targeted study. Thus, reducing 21st century insults to human health simply to a "mismatch" between the transition to agriculture and our biology is at best an unhelpful simplification. At worst it downplays the serious proximate effects of variations in the environment on individuals (Elton, 2008), including differential socioeconomic status and the inequality that results. Careful study of the archaeological, palaeoecological and palaeoenvironmental records will help to understand the proximate and ultimate factors that contributed to health in the past, which in turn will facilitate greater awareness of how to influence health status positively in contemporary populations.

The Holocene epoch is an interglacial (warm period) that succeeded the significant glacial period that reached a peak at ~20000BP (before present), after which northern hemisphere ice sheets started to retreat and sea and moisture levels rose. A short and abrupt cold period, the Younger Dryas, which started at ~12900BP and ended at 11700BP, marked the end of the late Pleistocene and the beginning of the Holocene. Within the Holocene, temperatures fluctuated, and include a warming period (the Holocene Climatic Optimum [HCO] between ~9000 and 5000BP), and several colder pulses known as Bond Events (Bond et al., 1997). The first cold Bond Event at 8200BP is cited as having a significant impact on farming groups in the Near East and Europe (e.g., Roffet-Salque et al., 2018). The significance of the HCO and the cold Bond Events has recently been correlated both to the collapse and development of different cultures in Ukraine (Nikitin 2020). Other studies have suggested that far from the 8200BP event causing collapse, site abandonment, and migration, the early farming communities of southwestern Asia showed resilience to abrupt and severe climate change (Flohr et al., 2016). For the Near East, the impact of the 8200BP event can be seen in changes in husbandry and consumption practices at Çatalhöyük East, with visible reductions in cattle herd sizes accompanied by an increase in caprine (sheep/goat) herd sizes (Roffet-Salque et al., 2018). Such shifts are wholly consistent with adaptability and resilience.

In general, the shift from the Late Glacial into the Holocene saw a marked improvement in the environments of Europe, with expansion of warmth-loving species (humans included) from glacial refugia, and the replacement of open grassland habitats with closed canopy deciduous woodlands alongside expansion or contraction of specific ecoregions or zones, such as the forest / forest steppe in Ukraine. Khotinsky (1984) notes that in the former USSR, the Late Glacial is characterised by a continental climate, with evidence for hyperzonality, i.e., a mixture of tundra, forest, and steppe environments (with some taxa that are found in present day steppe and desert zones), determined by water drainage and whether the land was north or south facing. In the Holocene there was a relatively rapid shift to more homogeneous zonal environments, with bands of tundra, forest, and steppe, in the pattern that is more familiar today (Khotinsky, 1984). During the Mesolithic period, the zones were characterised by tundra in the northern parts of the former USSR (Union of Soviet Socialist Republics), steppe in the southern regions, and a belt of birch, pine, spruce, and larch forest in between.

There was an expansion of temperate forests during the Mesolithic, but Ukraine lacks direct evidence for plant-based subsistence strategies (for example, as outlined by Zvelebil [1994] for some other Mesolithic sites in Europe). Exploitation of grasses in Ukraine at this time has been inferred from indirect evidence, such as sickle gloss or cereal imprints in pottery (e.g., Zvelebil and Dolukhanov, 1991). Nonetheless, the veracity of the identification of cereal imprints in relation to domesticated species and the adoption of agriculture in Ukraine has been questioned by the recent work of Motuzaite Matuzeviciute (2020), with the earliest evidence for domesticated cereals being linked to the appearance of the Linearbandkeramik culture in western Ukraine in the second half of the 6th millennium BCE. However, Motuzaite Matuzeviciute (2020) notes that the extent of these influences remains to be determined and that only limited evidence of cereal use, attributed to the Sredny-Stog culture, exists for eastern Ukraine prior to the 4th millennium BCE.

As might be anticipated, alongside the shifts in vegetation at the Pleistocene–Holocene transition, we see concomitant changes in the nature of the biomass, seasonality in resource availability, and a shift away from the large herds of animals, such as reindeer, mammoth, bison, and giant deer, which characterised the more open landscapes of the Late Glacial to less easily exploited solitary animals or small herds (e.g., aurochsen, red deer, wild horse and wild donkey, gazelle, mountain goat, wild boar, elk, and brown bear) that occupied the steppe, forest, and tundra zones (Zaliznyak, 2020a, b). In addition, it has been noted that during the Mesolithic period, fishing and plant gathering increased in importance compared to hunting (Dolukhanov and Khotinskiy, 1984). In essence, despite a broad range of species being available for exploitation, the nature of the landscape changes meant that the larger game animals were more dispersed in the environment and less predictable in terms of their availability than in the Late Glacial period. This necessitated a concomitant shift in the nature of food procurement strategies on the part of human groups and changes in the nature of the toolkits that were used in subsistence and other tasks (e.g., Lillie, 2015). Such a switch in subsistence activity may have had important implications for human adaptation and health.

7.2 Environments and health status along the Dnieper River

We focus on the Dnieper Rapids region of Ukraine, which preserves large cemetery populations, many belonging to the Neolithic Dnieper-Donets culture that spans the period 10400—5470calBP (~10000—3500calBCE). These cemeteries provide the opportunity for in depth study of palaeopathological evidence alongside stable isotope data to provide dietary context, within a region for which palaeoenvironments are generally well understood. Our case study concentrates on four cemeteries (the Epipalaeolithic cemetery of Vasilyevka III, the Mesolithic cemetery of Vasilyevka II, and the Neolithic (Mariupol-type) cemeteries of Yasinovatka and Dereivka I [Figure 7.1]) where the dating, pathological, and stable isotope data provide detailed insights into individual life histories and population dynamics.

<<FIGURE 7.1 NEAR HERE>>

Vasilyevka III is located on the left bank of the Dnieper, to the south of the town of Dniepropetrovsk, and is dated to 10400—9920calBP (10,000 to ~9300calBCE) (Jacobs, 1993, Lillie et al., 2003), at the Late Glacial – Holocene transition, with evidence that it was in use into the Mesolithic period at ~8850calBP (8280—7967calBCE) (Matthiesen et al., 2017). During the periods that Vasilyevka III was being used for interment (probably the final stages of the Younger Dryas, with temperatures rising into the Holocene, plus the early Holocene itself), a cool/dry to warm/dry climate persisted. The environment is initially characterised by poorly watered steppe away from the river valleys in the southern part of Ukraine (the Black Sea lowlands), with a central belt of forest-steppe, and the Polissya forest lowlands in the North (Zaliznyak, 2020a). During the period ~9000—5000BP temperatures increased across the northern hemisphere, reaching a peak at ~8000BP. Significant warming marks the onset of the earliest Holocene in Ukraine, and the cool climate and moist soils promoted the expansion of birch-pine in the north and the expansion of pine in the south, with birch-pine woodlands extending ~150km along the left bank of the Dnieper (Zaliznyak, 2020b).

As noted by Zaliznyak (2020b), the extent of the changes across the Pleistocene—Holocene transition were not as marked in the southern part of Ukraine as the north, although the loss of the cold-tundra forests resulted in the disappearance of herd animals such as bison, saiga, and donkey in the Black Sea lowland zone (Zaliznyak, 2020b). In general, the early Holocene in Ukraine at 10,300BP is characterised by decreased continentality and a reduction in hyperzonality (Velichko, 1973 cited by Dolukanov and Khotinskiy, 1984). By ~8,000 BP there was a transition to a more humid, increasingly warm, and differentiated landscape. At this time, broadleaved forests expanded into the lower Dnieper valley and steppe cover became more mesophilous (Kremenetski, 1995), with vegetation that preferred more moderate climates. At ~8200 BP (~8000BP in northern Eurasia), a Bond event (Bond et al., 1997) ushered in a period of dry and cold conditions for a period of ~60 years, with a milder interval of a few decades followed by progressive warming that took ~70 years (Kobashi et al., 2007; Thomas et al., 2007). However, whilst it has been suggested that this may also have occurred in the lower mid-latitudes, much farther south than previously thought, the actual impacts of this remain to be established, and the climatic fluctuation itself may have simply been an element of longer-term climatic instability (Wainwright and Ayala, 2019).

Vasilyevka II is located on the left bank of the Dnieper, in the Rapids region near the village of Vasilyevka, and is dated to the later Mesolithic at 9190—8020calBP (~7000—6200calBCE) (Telegin and Potekhina, 1987; Lillie and Jacobs, 2006). Based on the available dating, the Vasilyevka II assemblage at the Dnieper Rapids occurred at a time when the climate was nearing its optimum, which was reached between 6000 and 4600BP. At this point, the steppe vegetation became more mesophytic (adapted to neither particularly dry nor wet environments) when compared to that of the early Neolithic periods (cf. Dolukhanov and Khotinskiy, 1984). The period leading up to the climatic optimum appears to be reflected in the increased concentration of cemetery activity in and around the Dnieper Rapids region across the later Mesolithic and Neolithic periods. However, currently there is very little evidence to suggest that the 8200BP Bond event exerted any tangible impacts on the populations exploiting the Dnieper region, beyond the fact that the cemetery evidence is limited across the period of inferred climatic instability.

The Neolithic Mariupol-type cemetery of Yasinovatka is located on a high terrace ~25—30m above the left bank of the river, near the Dnieper Rapids. It is dated to 7476—6990calBP (~5800—4780calBCE) (Lillie, 1998a; Lillie et al., 2009). In contrast, the Neolithic Mariupol-type cemetery of Dereivka I is located on the right bank of the Omelnik river at the point where it joins the Dnieper near the village of Dereivka, ~120 km upstream of the other sites included in our case study. It is dated to 7253—6700calBP (~5270—4750calBCE), although this site also contains Mesolithic burials, with a date of 8340—7875calBP (6360—5879calBCE) on burial 84 (OxA-6161) (Lillie 1998a, Lillie et al., 2009). This site is located closer to the forest-steppe boundary at this time, but it is feasible to suggest that the conditions adjacent to the Dnieper may well have been similar throughout its middle and lower reaches due to the existence (and persistence) of forests along the valley throughout the periods discussed. However, we might anticipate some differing isotope values for biota at the forest-steppe boundary when contrasted with those encountered in the steppe zone near the Dnieper Rapids, irrespective of the forested nature of the river valley itself.

Both Neolithic cemeteries in our case study were established in the period of climatic stability between the 8200 BP and the 6300 BP Bond events, and indeed there are probably seven cemeteries in total that were established at the Rapids, or at the edge of the forest-steppe zone, during this period. This may well reflect the fact that optimum conditions existed for the expansion of populations into the region across this period, as the available dating indicates that activity and settlement along the Dnieper continued past the 6300 BP Bond event.

In the following "cemetery sections", we focus on stable isotope data for diet and palaeopathological evidence for compromised health, for both males and females. Most of the palaeopathological evidence is documented on dentitions, with other conditions less frequent or altogether absent. Further information about skeletal preservation and other aspects of the sites and material can be found in the relevant cited literature. It should be noted that the excavations generally revealed excellent preservation of the cranial region, and the cranial material was preferentially curated in the collections available for study. There was differential postcranial preservation, and (for dating purposes) only certain long bones were retained. Due to the free-draining nature of the loess soils, the postcranial material often could not be lifted, and age and sex estimation was undertaken in situ.

7.2.1 Vasilyevka III

Forty-four individuals were originally excavated from this cemetery, with 21 individuals available for study. These 21 individuals comprised ten males, nine females, one "sub-adult" individual and an individual of indeterminate age and sex (Lillie et al. 2003). The palaeopathological evidence suggests that the individuals at Vasilyevka III consumed protein-rich diets (attested to by calculus deposition on their teeth; Hillson 1979), with no evidence for the consumption of cariogenic foodstuffs such as carbohydrates or soft sticky foods (given the complete absence of caries on the teeth). Low levels of sub-optimal juvenile health are indicated by infrequent occurrences of enamel hypoplasia (Goodman et al., 1984a and b; Goodman and Armelagos, 1985a and b). The rates of expression of these non-specific indicators of juvenile physiological stress suggest that, in general, the human groups in the Dnieper region were probably not overly stressed in their growing years, in dietary terms at least. The age distribution of the incidence of the enamel hypoplasias suggests that prolonged weaning, through to the ages of 4.0—5.5 years, may have been in place for this population, with occasional instances of sub-optimal health prior to this age range (e.g., a female and a male individual who exhibit hypoplasia correlated to ~3—3.5 years of age), perhaps reflecting causes (e.g., sub-optimal living conditions) unrelated to the post-weaning diet (Lillie, 1998a). There was no indication of porotic hyperostosis/cribra orbitalia on any of the crania examined from Vasilyevka III (Lillie 1998a).

Stable isotope analysis of 21 individuals from Vasilyevka III (Lillie et al., 2003) produced results for 14 individuals. The average $\delta^{13}C$ value was -22.2±0.2‰ and average $\delta^{15}N$ value was 12.7±0.6‰ (Lillie et al., 2003), which indicate a diet with a significant input from freshwater resources, which links straightforwardly back to the evidence for calculus deposition on the detentions studied. This is perhaps unsurprising given the position of these cemeteries close to the Dnieper Rapids, giving direct access to freshwater resources. Interestingly, two of the three individuals with the highest nitrogen isotope values at Vasilyevka III were from males aged 50+, perhaps suggesting that these older people were consuming diets that comprised significant inputs of fish, a soft foodstuff. The fact that a female aged 18—22 exhibits the second highest nitrogen value of 13.10‰ is less easy to interpret in this context (i.e., she is not an old individual), but the value is not too much higher than other females in the skeletal sample, which range from 11.66 to 13.10‰ (six individuals). This may indicate that whilst males may have hunted, perhaps expending a lot of energy for unpredictable returns, females were exploiting a more reliable and easily accessible food resource through fishing. In addition, the older male individuals in the society, who were potentially no longer able to hunt, were also involved in these activities in some way.

At Vasilyevka III, Nuzhnyi (1989, 1990) identified evidence for interpersonal violence on five of the individuals from the cemetery population, with arrowheads and slotted bone points in association with the remains. In two instances, the deceased had microliths embedded in their lumbar vertebrae, indicating that they had been shot in the back, and another individual had arrow and spear points embedded in their skeleton. Furthermore, at the cemetery sites of Vasilyevka I and Voloshkoe, evidence for impact damage from arrows has also been recovered. Whilst these latter cemeteries remain undated in absolute terms, the stratigraphic context and type of artefacts led Nuzhnyi (1989, 1990) to suggest that they are broadly contemporary in chronological age with Vasilyevka III. The evidence for interpersonal violence may well indicate increased competition for resources at the Late Glacial to Holocene transition in the region, and the positioning of the cemeteries at the Rapids could be interpreted as an assertion of ancestral rights of access to the reliable freshwater resources available at this location (Lillie 1998a).

Overall, despite the chronological position of Vasilyevka III near the Late Glacial – Holocene boundary, the data suggest that there is minimal evidence for dietary stressors in the skeletal remains studied and that whilst there is good evidence for the consumption of protein-rich diets, the complete absence of evidence for dental caries indicates that cariogenic foodstuffs were not integral to the diet of these individuals. Perhaps the most important indicator of some form of "stress" in terms of access to resources is the prevalence of bone damage related to interpersonal violence and the fact that the cemeteries themselves are located at the Dnieper Rapids, in a riparian (riverbank) environment where a broad range of resources were available for exploitation.

7.2.2 Vasilyevka II

Demographic and palaeopathological analyses of the Vasilyevka II cemetery population (14 individuals [five females and nine males]) demonstrate that they lived well past the mean average life expectancy for the Mesolithic period, with three individuals (two males and a female) reaching the 50—60 year age bracket at death (assessed via molar wear seriation and cranial suture closure), and a further three males and one female surviving into the

40—50 year age category. Interestingly, one of the older males also has evidence for healed cranial surgery (trepanation) and linear enamel hypoplasia on the left upper 1st molar (Lillie, 1998b). This hypoplastic event correlates with a non-specific metabolic disruption occurring at 2.0—2.5 years of age (Goodman et al., 1987). Despite this childhood stressor, this individual clearly lived to a mature age, and even subsequently survived the surgical intervention associated with a trepanning procedure (Lillie, 1998b).

At Vasilyevka II, there is no evidence for caries on the dentitions of this group, nor porotic hyperostosis, an indicator of anaemia of potentially many causes, such as infection (Lillie, 1998a; Stuart-Macadam, 1992). To assess protein consumption, the preserved teeth (n=324) were studied for calculus deposition, although 147 teeth could not be considered due to factors such as exhibiting postmortem damage, advanced functional-related wear affecting the crowns (where calculus mainly accumulates), or a low functional age (i.e., the individual was below ~24 years of age and calculus deposition was not evidenced). Despite these limitations, all male teeth that could be studied exhibited calculus, whilst females had more teeth with no evidence for calculus deposition. There are limitations to the data in that there are no females represented in the 25—40 year age categories and, whilst the population analysed is small, the lack of females in these age groups is unusual (Lillie, 1998a).

There is a clear lack of evidence on the dentitions for the consumption of dietary foodstuffs that would have initiated dental caries and, as only one individual exhibited a single hypoplasia, there is also a lack of evidence for childhood stress at Vasilyevka II. The presence of postcranial skeletal remains at Vasilyevka II offers a rare opportunity for the study of pathology in this region of the skeleton, as skulls usually dominate in the curated Dnieper Rapids human remains, due to preservation issues in the loess soils of the steppe region. The only other pathological evidence on these remains was osteoarthritis, which was visible on the joints of the left femur, humerus, and ulna of one individual. Meiklejohn and Zvelebil (1991) previously noted that osteoarthritis is the most common pathology found on Mesolithic post-cranial skeletal remains in Europe. The evidence of disease from Vasilyevka

II is limited due to the small number of individuals, but the data do conform to the generally low levels of pathology that were in evidence at Vasilyevka III.

Stable isotope analysis carried out on 14 individuals from the cemetery of Vasilyevka II (Lillie and Jacobs, 2006) revealed isotope ratios with a mean of -20.94±0.49‰ for $\delta^{13}C$ and 13.39±0.62‰ for $\delta^{15}N$, with the individual with the highest $\delta^{15}N$ value being a male aged 20—30 years. The Vasilyevka II individuals all have $\delta^{15}N$ values above 12.35‰, and the data indicate relatively uniform diets among males and females, with freshwater fish and animal proteins being important dietary elements (Lillie and Jacobs, 2006). The $\delta^{15}N$ values from Vasilyevka II differ slightly from the Epipalaeolithic—Earlier Mesolithic values from Vasilyevka III, with the later Mesolithic values at 13.39±0.62‰ being higher when compared to the chronologically earlier values of 12.47±0.61‰. The elevated nitrogen from Vasilyevka II may indicate a higher input from freshwater fish in the later Mesolithic when compared to the Epipalaeolithic period. The $\delta^{13}C$ value, at -20.94±0.49‰, is more positive than at Vasilyevka III where values of -22.2±0.2‰ are recorded. This shift may well reflect variations in the resources that were available for exploitation by the populations in this region of Ukraine, linked to the changing environments that occurred during the time that Vasilyevka II was in use (Velichko et al., 2009; Kotova and Makhortykh, 2010; Budd and Lillie, 2020).

7.2.3 Yasinovatka

There were 68 individuals excavated from the Neolithic cemetery of Yasinovatka across its use. The cemetery area was identified as a sub-rectangular pit which was highlighted by red staining associated with the ochre applied to Neolithic burials in the region (Telegin and Potekhina, 1987). Two distinct burial contexts were distinguished, with a number of discrete grave pits of oval form overlain by a large collective burial pit. For the current study, 31 individuals with preserved teeth were assessed (comprising 20 males, six females and five individuals of indeterminate biological sex, although two individuals had teeth that were too worn to allow detailed study) (Lillie 1998a, Budd et al., 2020). No carious lesions were identified in the preserved dentitions, again suggesting that their diet was high in proteins and/or low in carbohydrates. At this cemetery, only one of the studied individuals lacked calculus (the presence of which in archaeological remains is generally common) and six of the 31 individuals studied had evidence for enamel hypoplasia. Of the individuals with calculus, all males and females exhibited deposits across the grades, from light to heavy, although a substantial number of teeth (130/441) had no evidence for any calculus despite some high functional ages (i.e., older than ~45 [Lillie 1998a]). The timing for enamel hypoplasia formation appeared variable, occurring as early as 2.5 years of age in some individuals, and later (up to 5 years) in others, suggesting that low levels of juvenile stress were occurring in early childhood. However, this cannot be reliably linked to weaning stress, as opposed to any of the other childhood stressors that might cause hypoplasia, such as hypoparathyroidism, and vitamin A and D deficiencies, fever, maternal diabetes, neonatal asphyxia and jaundice, nephrotic syndrome, and gastroenteritis (Goodman et al., 1984a, b; Goodman et al., 1987; Goodman, 1993; Seow, 1997, 2013).

Interestingly, statistical analysis of the observed versus expected frequencies of calculus for males versus females at Yasinovatka (Lillie, 1998a) highlights a reversal in the general trends observed for the remainder of the skeletal series from the Dnieper region. Namely, it is the females who exhibit the highest prevalence of heavy calculus. The fact that an 18—25 year old female exhibits heavy calculus deposition suggests preferential access to dietary proteins for females from an early age. Such heavy deposits would suggest high protein intakes, as would the overall wider distribution of calculus seen in individuals from Yasinovatka. As males outnumber females at a ratio of 4:1 in the assemblage studied, this observation suggests that the male—female expression of calculus at Yasinovatka reflects the consumption of (at the very least) equivalent levels of protein-rich foodstuffs between the sexes in this cemetery population. However, it is tempting to suggest that at Yasinovatka, females are central to securing dietary protein, potentially through fishing, and/or that the males at this site are not actively engaged in the procurement of dietary proteins to the same degree as females. Obviously, caution is needed given the low numbers of individuals available for study, but some intriguing trends appear at Yasinovatka that are not seen elsewhere in the skeletal series studied to date.

Where crania were preserved (24 individuals), no evidence for cribra orbitalia or porotic hyperostosis (bone changes in the orbits and on the cranial bones, respectively) was found and, despite the fact that fish and deer tooth pendants are ubiquitous in the burial inventory at Yasinovatka, levels of fish consumption do not appear to have resulted in increased parasitic infestation (e.g., Seow 1997, 2014). As this observation runs contra to the evidence from Dereivka I (considered below), we might hypothesise that the group using Yasinovatka as a burial ground were perhaps more peripatetic than the people who were burying their dead at Dereivka I.

At Yasinovatka, samples from 38 individuals produced reliable isotope measurements. These results, with $\delta^{13}C$ at -22.3±0.9‰ and $\delta^{15}N$ at 13.7±1.5‰, are commensurate with data from the site of Nikolskoye (another key Mariupol-type cemetery that fully overlaps with the dating evidence from Yasinovatka and Dereivka), and are more positive than those from Dereivka I. The data indicate that freshwater aquatic proteins formed the mainstay of the diet at Yasinovatka (Budd et al., 2020). The material culture inventory from Yasinovatka includes bivalve shells and teeth of freshwater fish (Telegin and Potekhina, 1987), and as many Dnieper-Donets Mariupol-type cemeteries have evidence for the exploitation of these resources, these data reinforce the importance of, and dependence on, the freshwater environment (Lillie, 2020; Budd and Lillie, 2020). Nonetheless, as has been recorded at other locations, there is variation among the population. Two individuals produced lower values than most of the population analysed. A young adult male (aged 18—25), who stands out in having decorative plates of boar tusk that appear to have been sewn on to the arm of his clothing, produced a $\delta^{13}C$ value of -23.6‰ and a $\delta^{15}N$ value of 11.4‰, and a female aged 20—25, had a $\delta^{13}C$ value of -22.4‰ and a $\delta^{15}N$ value of 7.4‰. There is clear variability in diet at Yasinovatka and, in the latter two individuals, C_3 terrestrial proteins formed the basis of their diets, although the lower $\delta^{15}N$ value of the female suggests she ate proportionately less animal protein than the male. Recent assessment of this cemetery (Budd et al., 2020) has also suggested that these individuals may have been consuming terrestrial plants and animals from areas away from the Rapids, i.e., that potentially they were recent immigrants into the region. Intriguingly, these individuals date as the earliest burials at Yasinovatka (Lillie et al. 2020).

7.2.4 Dereivka I

For the Neolithic period, the site of Dereivka I offers insights into dietary pathways away from the concentration of cemeteries that are located ~120km downstream at the Dnieper Rapids. This is the largest Mariupol-type cemetery in the Dnieper system. This site also stands out from the other cemeteries studied by Lillie (1998a) in that it is the only location where the palaeopathological evidence highlights a combination of a degree of sedentism associated with what appears to be an increased risk of parasite loading. A total of 104 adult individuals were excavated, and 62 individuals, comprising 42 males, 13 females and 7 individuals of indeterminate biological sex, were analysed by Lillie (1998a). As with the other cemeteries in the Dnieper region, there is a complete absence of caries on the dentitions of the individuals studied. However, calculus is again in evidence, although at this location all the individuals with teeth exhibited some degree of calculus deposition. In relation to the rates of calculus, an interesting aspect of the dentitions from Dereivka I is the fact that five individuals in the younger age range (12—22 years) have lower levels of calculus deposition than the five people in the 18—25 age category. This distribution suggests heavier protein consumption patterns for some than have generally been recorded elsewhere in the cemetery samples studied. Importantly, statistical analysis indicates that male-female expression of calculus is equivalent (Lillie, 1998a), suggesting that equality in access to dietary protein is occurring at Dereivka I. This dietary equivalence may also help to account for the single instance of enamel hypoplasia, indicative of a non-specific childhood stress event.

At Dereivka I, a total of 80 individuals were represented by preserved crania suitable for the study of pathology and, of this number, four (5% of the cemetery population) had cribra orbitalia (Hengen, 1971; Stuart-Macadam, 1991, 1992). When coupled with the absence of corresponding osseous involvement in the facial region, the levels of cribra orbitalia recorded at Dereivka I indicate that hereditary causes, haematological and circulatory disorders can be discounted as the cause for lesion development; this is because the population-based expression exceeds 1% (cf. Klepinger, 1992). Whilst several factors may have influenced cribra orbitalia development (Stuart-Macadam, 1989; Walker et al., 2009), the dependence on fish in the diet of these people at Dereivka, coupled with increased sedentism, could have led to increased pathogen loads (fish-borne parasites) and the initiation of an adaptive response in the immune system (cf. Kent, 1986; Macchiarelli, 1989; Stuart-Macadam 1992; Walker 1986). Evidence from elsewhere in Europe, such as the Danish Ertebølle and Danubian Iron Gates, has demonstrated that a heavy reliance on aquatic/marine resources can lead to reductions in the quality of fisher-forager diets due to parasite infection (Meiklejohn and Zvelebil 1991), and the evidence from Dereivka I lends additional support to these observations.

At Dereivka I, which lies at the boundary between the forest-steppe and steppe zones, the atypical nature of the pathologies discussed above are not reflected in the isotope ratios that have been recorded to date (Lillie et al., 2011; Budd and Lillie, 2020). Of the 104 individuals available for study, so far only thirteen have been analysed for diet using stable isotope analysis. The results for $\delta^{13}C$ and $\delta^{15}N$ are -23.2±0.6‰ and 12±1‰, indicating that aquatic proteins did contribute a significant proportion to the diet at Dereivka, but these values are lower than those for the earlier Mesolithic site of Vasilyevka II, and they are in fact lower that those found at Yasinovatka and Nikolskoye, at 13.4±0.6‰ (Lillie et al., 2011; Budd et al., 2020). Budd and Lillie (2020) have argued, based on the diet isotope data, that the location of Dereivka, ~120km to the northwest of the Rapids sites, near the forest-steppe boundary, and on a tributary of the Dnieper, may potentially have facilitated access to different fish species, and also to a broader spectrum of terrestrial plant and animal species.

The nitrogen isotope values from two individuals at Dereivka I, at 9.9‰ and 10.5‰ respectively, suggest that some of the individuals consumed diets that were focussed on terrestrial resources (Lillie et al., 2011). As one individual from this site has been shown to group with Anatolian and European Neolithic farmers at the whole genome level

(Mathieson et al., 2018), it is entirely feasible that at this relatively early date in the Neolithic of the Dnieper region we are seeing the first immigration of individuals with southwestern origins into this steppe region. The fact that Dereivka I is at the forest-steppe to steppe boundary, at a location that mirrors the subsequent spread and distribution of the Trypillia farming culture in Ukraine, may well be more than mere coincidence. As such, we might hypothesise that variability in diet at Dereivka I could indicate a shift towards a more terrestrial resource focussed subsistence strategy, at least for some individuals, occurring at a time (7253—6700calBP (4949—4799calBCE)) when the initial stages of contact with western farmers were happening in this region.

7.3 Discussion

Using the evidence from the Dnieper River region in Ukraine, we attempt to disentangle the climate/environmental and archaeological data with a view to identifying significant impacts on the socio-cultural and economic trajectories of the groups in this region across the period 10400—5700calBP (~10,000—3800calBCE), and in turn assess how these may have influenced evolutionary fitness. The data underline that even in a small geographic area and relatively short period of time (~6000 years or so), human diets varied within and between groups, even if the basic spectrum of available resources was similar. In the Dnieper region red and roe deer, elk, aurochs, and wild boar were all hunted across the Mesolithic period, as seen in faunal evidence, and archaeological evidence further attests to the exploitation of freshwater resources such as carp, pearl roach, and freshwater molluscs (Telegin and Potekhina, 1987). This is consistent with other Mesolithic sites in central and eastern Europe. At Zvejnieki in Latvia, Larsson et al. (2017:60) report that elk and beaver dominate the faunal remains at this Mesolithic settlement site, while pike is the most common fish species. The Danubian Iron Gates sites (Serbia and Romania) have evidence for the consumption of sturgeon, carp, catfish, and freshwater mussels (Cook et al., 2009). Whilst C_3 terrestrial resources such as red deer, aurochs, and wild boar were important, Bonsall et al., (2015:696) have argued that substantial amounts of fish were consumed by the Iron Gates populations at Vlasac, Lepenski Vir, Hajdučka Vodenica and Padina across the Mesolithic, with the possibility that marine resources (including sturgeon) increased in importance during the later Mesolithic period (Cook et al., 2009). In Karelia and north-western Russia, Mesolithic economies were oriented towards the hunting of forest animals (such as reindeer, red deer, boar, and beaver) and waterfowl, with fishing also being of some importance (Dolukhanov, 2017). Indeed, it has been argued that “fishing and gathering were of great importance everywhere” in the forest zone of the former USSR (Dolukhanov and Khotinskiy, 1984:321).

Fish certainly comprised an important part of the diet in the Dnieper region across the Epipalaeolithic (the transitional period at the very earliest part of the Holocene) through to the Eneolithic (the period at the junction between the latest Neolithic and Copper Age) periods (Lillie and Richards, 2000; Lillie et al., 2003; Lillie and Jacobs, 2006; Lillie et al., 2011; Budd and Lillie, 2020; Budd et al., 2020). However, the stable isotope data reviewed here indicate that these resources were not of equal importance for all people and all groups. Older males at Vasilyevka III seemingly ate more fish than did other members of that population (possibly because of ease of mastication) (Lillie, 1998a, 2020). A couple of individuals at both Dereivka I and Yasinovatka had diets dominated by terrestrial rather than aquatic foodstuffs. All people at Vasilyevka II had a greater emphasis on fish in the diet than those at the earlier site of Vasilyevka III and the later site of Dereivka I. This may reflect the preferences of people in those different groups. There is a wealth of ethnographic data indicating that humans do not simply eat the foods available to them, but make cultural choices about their diet, governed, among other things, by symbolic value, prestige, and enculturated taste (see review in Ulijaszek et al., 2012). However, it may also reflect short term shifts in resource availability that could have been caused by the climatic fluctuations, or Bond events, occurring between ~8200 and 6300 BP.

Across the early to mid-Holocene the climate, environment, and landscape of central and eastern Europe are characterised by relative stability punctuated by a series of global and localised climatic perturbations that vary in their duration, severity, and potential impacts on human populations, which are identified in part by differences in stable isotope signatures in the humans living in the region. The difference in diet at Vasilyevka II (8200—

8020calBP) might be a response to the developing Bond cooling event that occurred around 8200BP. This could be because patterns of terrestrial mammal availability shifted, forcing a greater reliance on fish. Although the geographic distribution of freshwater fish will shift with long-term thermal changes, fish initially respond to temperature changes through shifts in behaviour and microenvironment within a given water source (Pletterbauer et al., 2018). Therefore, whereas the marked environmental shift that characterised the Late Glacial to the Holocene period led to a significant restructuring of the available biomass (and by extension human subsistence) (Dolukhanov, 1997), the opportunism and flexibility that has such a long evolutionary history in hominins (Elton, 2008; Potts, 1998; Ulijaszek et al., 2012) potentially facilitated a shorter-term dietary response to the more modest climatic perturbations of the Holocene.

One important question for those interested in evolutionary medicine, and indeed human health and disease more generally, is how that short-term variation may have influenced health outcomes, proximately and ultimately. The available palaeopathological data from the Dnieper series indicate generally low rates of pathology, although caveats obviously exist in relation to the absence of curation of postcranial remains due to factors such as preservation (Lillie 1998a). The pathologies in evidence accord well with known rates of pathology identified in hunter-gatherer skeletons excavated from sites in central and northern Europe. In those groups, outside of the Mediterranean region, caries rates are generally low (Meiklejohn and Zvelebil, 1991). The age at which stress episodes occur in the Dnieper series (evidenced by enamel hypoplasias) is commensurate with Mesolithic populations elsewhere, such as those at Skateholm I and II (Meiklejohn and Zvelebil, 1991; Lillie 1998a). This indicates that, overall, there was no health and, by implication, fitness, cost or benefit to small variations in diet over time and space. However, a combination of the diet consumed and human behaviour may have resulted in adverse health outcomes. The identification of cribra orbitalia at Dereivka I is not unusual for a population exploiting fish resources wherein increased pathogen (parasite) loads could have been present. This situation is especially significant given the fact that the Dereivka population appears to have been more sedentary than the groups downstream in the Dnieper system at the Rapids, and the temporally overlapping group at Yasinovatka. Although early exposure to parasites may help to prevent autoimmune conditions (the "Hygiene Hypothesis"; see Chapter 11), long-term research on contemporary hunter-gatherer populations suggests that parasite load increases interbirth intervals and reduces overall health and well-being, potentially impacting on evolutionary fitness (Hurtado et al., 2008).

The concept of "transition" is influential in evolutionary medicine. It is closely aligned to "mismatch", with the former often argued to lead to the latter. When thinking about palaeodiets, the transition from mobile hunting and gathering to a sedentary agrarian existence is emphasised. The Neolithic is often viewed as a transition point, with hunting and gathering giving way to a more sedentary agrarian subsistence pattern. Whilst influences upon cultural evolution are exerted by a range of mechanisms including social, economic, and ecological variables, there is little doubt that the relative significance of these factors varied across the transition from the late Pleistocene to Holocene periods throughout Europe (Dolukhanov, 1984; Dolukhanov and Khotinskiy, 1984). Being located between western and eastern Europe, Ukraine experienced influences from incipient farming cultures in the west from ~6500calBCE onwards. However, the rate of spread and adoption of farming is protracted and variable in both a west-east direction and a south-north direction such that, whilst contacts with farming groups are increasing across the latter part of the seventh millennium and into the sixth millennium BCE in the south and west of Ukraine, populations to the east and north retain a fisher-hunter-gatherer subsistence lifestyle.

Lillie (1998a) has previously suggested that if not for the differences in material culture, there is little to distinguish the skeletal remains from Mesolithic sites from those of the early Neolithic period in the Dnieper region of Ukraine. These populations were clearly following very similar lifeways, with a reliance on freshwater resources continuing from the Epipalaeolithic at Vasilyevka III through to the end of the Neolithic period and into the Eneolithic period in this region. The Dnieper-Donets populations who buried their dead in the Mariupol-type cemeteries align closely with Mesolithic groups in the Danube and Baltic regions. However, at the Neolithic transition, whilst some aspects of material culture suggest that changes are occurring, unlike in areas to the west, these populations retain the essentially Mesolithic subsistence strategies that are attested at sites like Olenii Ostrov in Karelia and Zvejnieki in Latvia. At the former site, recent stable isotope analysis (Budd and Lillie, in prep) has shown that the Mesolithic individuals interred at this location have elevated nitrogen ratios that are fully commensurate with those in evidence at Mesolithic sites in the Danubian Iron Gates sites (e.g. Vlasac and Schela Cladovei; Cook et al., 2009; Lillie et al., 2011), the Mesolithic period burials at Zvejnieki in northern Latvia (Eriksson et al., 2003), and the Dnieper Rapids series (Lillie et al., 2011; Budd and Lillie, 2020).

In the context of transition, it is the change in terrestrial biomass between the Pleistocene and Holocene that is more important for diet and behaviour in the Dnieper Rapids region than the shift between the Mesolithic and Neolithic periods. The increasing importance of aquatic resources in the Mesolithic came about because of the increasingly dispersed nature of large game animals and the need to exploit a “broader spectrum” of resources (Binford, 1968; Flannery, 1969). Of course, exploitation of small game and fish was not a new phenomenon in the Mesolithic and had its roots in the Pleistocene (see review in Ulijaszek et al., 2012), but its relative importance probably increased (sensu Stiner, 2001). This may have helped shape behaviour, with groups no longer travelling large distances following game herds but instead staying closer to home and extracting resources from a more settled and secure base (as seen in the Danube region [Bonsall et al., 1997; Cook et al., 2001, 2002, 2009; Bonsall et al., 2015]).

What the Mesolithic – Neolithic data from Ukraine indicate is that potentially adverse health outcomes may arise not from dramatic shifts in subsistence (the premise on which “Stone Age diet” arguments are built), but from small, potentially transient behavioural changes, such as a decrease in mobility in one group compared to another, that may interact with diet (or its indirect effects). All the groups represented in the Mariupol-type cemeteries in the Dnieper River region have the same fundamental diet, albeit with variations in the relative importance of terrestrial and aquatic resources. The palaeopathological data described here are largely homogeneous among these groups (and align with findings in other European hunter-fisher-forager groups), except for the evidence for cribra orbitalia at Dereivka. This health stress, and a condition that develops in the growing years of childhood, was not obvious from the dietary data, and it is only with the combination of archaeological, isotopic, and palaeopathological data that inferences about its cause can be made. In this case, a greater exposure to fish-borne parasites because of a probable increase in settled living is evidenced. What is interesting from an evolutionary perspective is that this was not a consistent, long-lasting change, or indeed one that was mirrored at the contemporary sites of Yasinovatka and Nikolskoye (the latter site continues in use until the Eneolithic transition in this region, 5700—5470calBP) (Lillie, 2020). Thus, although the reproductive success of the Dereivka population may have been adversely affected by increased pathogen load, there is no evidence that this was a consistent health risk in the Neolithic of the region that led to a long-term selective pressure. This in turn lends weight to arguments that, in many cases, we should not view changes of diet and human behaviour in terms of "revolutions" that promoted mismatch, and that we should also think about people's health through a proximate as well as an ultimate lens when considering how evolutionary approaches may inform our understanding of health, both in the past and today.

7.4 Conclusion

Undeniably, pathogens and diets have exerted selective pressures on humans, but variation and variability in environments and behaviours may have also applied profound pressures on humans, leading to selection for plasticity in morphology, physiology, and behaviour (reviewed in Elton, 2008). Plasticity has fitness advantages in rapidly changing environments and the potential range of responses within and among populations to varied and varying habitats and situations is so great that we must critique the notion of adaptation to a monotypic ancestral environment. However, this is not to say that plastic responses in all combinations have similarly beneficial or even neutral outcomes. The data we present here, based on a detailed examination of health and dietary indicators from populations on a small geographic and temporal scale, at a key juncture in human history, indicate that modest changes in behaviour may synergise to create adverse health outcomes. In this way, understanding the ecology of human populations may be as important as evolution in appreciating the trajectory of human health. Using the palaeopathological record to identify small scale differences in health among populations sheds light on these ecological differences. The take home message from the work described here is that although an evolutionary perspective over a long time-span provides undeniably important context, we must not overlook the impact of changes on a small, proximate scale that affects the health of individuals. For the most part, it is these proximate effects on individuals that are the subject of treatment by clinicians, and it is hard to see how this could be altered substantially without detriment to health and well-being. One key challenge for the future is thus to link proximate and evolutionary perspectives to improve our understanding of health in the past and to influence health status positively in contemporary populations.

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References

Aiello, L.C., Wheeler, P. 1995. The expensive tissue hypothesis: the brain and the digestive system in human and primate evolution. Current Anthropology 36: 199-221.

Beall, C.M. Two routes to functional adaptation: Tibetan and Andean high—altitude natives. Proc. Natl. Acad. Sci. USA. 2007;104(Suppl. 1):8655–8660. doi: 10.1073/pnas.0701985104.

Binford L.R. 1968. Post—Pleistocene adaptations. In: Binford, S.R. and L.R. Binford (eds.), *New Perspectives in Archaeology*. Chicago: Aldine, pp 313-341.

Bond, G., Showers, W., Cheseby, M., Lotti, R., Almasi, P., De Menocal, P., Priore, P., Cullen, H., Hajdas, I. and G. Bonani. 1997. A pervasive millennial scale cycle in the North Atlantic Holocene and glacial climates. Science 294:2130-6.

Bonsall, C., Lennon, R.J., McSweeney, K., Stewart, C., Harkness, D.D., Boroneant¸ V., Payton, R.W., Bartosiewicz, L. and J.C. Chapman. 1997. Mesolithic and Early Neolithic in the Iron Gates: a palaeodietary perspective. *Journal of European Archaeology* 5(1):50-92.

Bonsall, C., Macklin, M.G., Boroneant¸, A., Pickard, C., Bartosiewicz, L., Cook, G.T. and T.F.G. Higham. 2015. Holocene climate change and prehistoric settlement in the lower Danube valley. *Quaternary International* 378:14-21.

Boaretto, E. Wu, X., Yuan, J., Bar—Yosef, O., Chu, V., Pan, Y., Liu, K., Cohen, D., Jiao, T., Li, S., Gu, H., Goldberg, P. and S. Weiner. 2009. Radiocarbon dating of charcoal and bone collagen associated with early pottery at Yuchanyan Cave, Hunan Province, China. *Proceedings of the National Academy of Sciences* 106: 9595-9600.

Brown, T.A., Jones, M.K., Powell, W. and R.G. Allaby. 2009. The complex origins of domesticated crops in the Fertile Crescent. *Trends in Ecology and Evolution* 24:103-109.

Budd, C. and M.C. Lillie. 2020. The prehistoric populations of Ukraine: stable isotope studies of fisher-hunter-forager and pastoralist — incipient farmer dietary pathways. In: Lillie, M.C. and I.D. Potekhina (eds.). *Prehistoric Ukraine: From the First Hunters to the First Farmers*. Oxford: Oxbow Books Ltd. pp. 283-307. ISBN: 9781789254587

Budd, C.E., Potekhina, I.D. and M.C. Lillie. 2020. Continuation of fishing subsistence in the Ukrainian Neolithic: diet isotope studies at Yasinovatka, Dnieper Rapids. *Archaeological and Anthropological Sciences* 12(2):article id. 64. https://doi.org/10.1007/s12520-020-01014-4

Budd, C. and M.C. Lillie. *in prep*. Yuzhnyi Olenii Ostrov, Lake Onega, Karelia: first diet isotope analysis of the Mesolithic fisher-hunter-forager population. To be submitted to *Antiquity*.

Cohen, M. and Armelagos, G. (eds) 1984 Palaeopathology at the origins of agriculture. London, Academic Press

Cohen, M.N., and Crane-Kramer, G.M.M. 2007. *Ancient Health: Skeletal Indicators of Agricultural and Economic Intensification.* Gainesville: University Press of Florida.

Cook, G.T., Bonsall, C., Hedges, R.E.M., McSweeney, K., Boroneant, V. and P.B. Pettitt. 2001. A freshwater diet-derived ^{14}C reservoir effect at the Stone Age Sites in the Iron Gates gorge. *Radiocarbon* 43:453-60.

Cook, G.T., Bonsall, C., Hedges, R.E.M., McSweeney, K., Boroneanţ, V., Bartosiewicz, L. and P. Pettitt. 2002. Problems of dating human bones from the Iron Gates. *Antiquity* 76:77-85.

Cook, G., Bonsall, C., Pickard, C., McSweeney, K., Bartosiewicz, L. and A. Boroneanţ. 2009. The Mesolithic-Neolithic transition in the Iron Gates, Southeast Europe: Calibration and Dietary Issues. In: Crombé, P., Van Strydonck, M., Sergant, J., Bats, M. and M. Boudin (eds.). *Chronology and Evolution within the Mesolithic of North-West Europe*. pp. 497-515. Newcastle Upon Tyne: Cambridge Scholars Publishing. Proceedings of an International Meeting, Brussels, May 30th – June 1st 2007.

Cordain, L., Brand Miller, J., Eaton, S.B., Mann, N., Holt, S.H.A., and J.D. Speth. 2000. Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. *American Journal of Clinical Nutrition* 71:682-692.

DeMenocal, P.B. Plio-Pleistocene African climate. Science, 270, 53-59. 1995.

Dennell, R. 1983. *European Economic Prehistory: A new approach*. London: Academic Press.

Dobney, K. and G. Larson. 2006. Genetics and animal domestication: new windows on an elusive process. *Journal of Zoology* 269:261-271.

Dolukhanov, P.M. 1984. Upper Pleistocene and Holocene Cultures of the Russian Plain and Caucasus: Ecology, economy and settlement pattern. In Wendorf, F., and A.E. Close (eds.) *Advances in World Archaeology: Volume 1*. New York: Academic Press. pp. 323-58.

Dolukhanov, P.M. 1997. The Pleistocene-Holocene transition in Northern Eurasia: Environmental Changes and Human Adaptations. *Quaternary International* 41/41:181-191.

Dolukhanov, P.M. 2017. Postglacial human colonisation of Fennoscandia. In: Kotlyakov, V.M., Velichko, A.A. and S.A. Vasil'ev (eds.). Human Colonisation of the Arctic: The Interaction Between Early Migration and the Palaeoenvironment. pp. 7-14. London: Academic Press.

Dolukhanov, P.M. and N.A. Khotinsky. 1984. Human Cultures and the Natural Environment in the USSR during the Mesolihtic and Neolithic. In: Wright, H.E. and C.W. Barnosky (eds.), *Late Quaternary Environments of the Soviet Union*. pp. 319-27. Minneapolis: University of Minnesota Press.

Eaton, S. B. and M. Konner. 1985. Paleolithic nutrition. A consideration of its nature and current implications. *New England Journal of Medicine* 312: 283-289.

Eaton, S.B. and S.B.I. Eaton. 1999. The evolutionary context of chronic degenerative diseases. In: Stearns, S.C. (ed.), *Evolution in Health and Disease*. pp. 251-259. Oxford: Oxford University Press.

Eaton, S.B., Eaton, S.B. and M.J. Konner. 1999. Palaeolithic nutrition revisited. In: Trevathan, W.R., Smith, E.O., and J.J. McKenna (eds.). *Evolutionary Medicine*. Oxford: Oxford University Press. 313-332.

Elton, S. 2008. Environments, adaptation, and evolutionary medicine: should we be eating a Stone Age diet? In: Elton, S. and P. O'Higgins. (eds.), *Medicine and Evolution: Current Applications, Future Prospects*. pp. 9-33. Boca Raton: CRC Press.

Elton, S. 2016. Mismatch or mass marketing? Stone Age diets, industrialisation and ultra-processed foods. *Toplum ve Hekim (Community and Physician)* 31(5): 323-333.

Eriksson, G., Lōugas, L. and I. Zagorska. 2003. Stone Age hunter-fisher-gatherers at Zvejnieki, northern Latvia: radiocarbon, stable isotope and archaeozoology data. Before Farming 2003/1(2):1-25.

Flannery, K.V. 1969. Origins and ecological effects of early domestication in Iran and the Near East. In: Ucko, P.J. and G.W. Dimbleby (eds.), *The Domestication and Exploitation of Plants and Animals*. pp. 73-100. Chicago: Aldine.

Flohr, P., Fleitmann, D., Matthews, R., Matthews, W. and S. Black. 2016. Evidence of resilience to past climate change in Southwest Asia: Early farming communities and the 9.2 and 8.2 ka events. *Quaternary Science Reviews* 136:23-39.

Foley, R.A. 1993. The influence of seasonality on hominid evolution. In Ulijaszek, S.J., Strickland, S. (Eds.) Seasonality and Human Ecology, pp. 17-37. Cambridge: Cambridge University Press.

Foley, R.A. 1995. The adaptive legacy of human evolution: a search for the environment of evolutionary adaptedness. *Evolutionary Anthropology* 4: 194-203.

Goodman, A.H., 1993. On the interpretation of Health from Skeletal Remains. *Current Anthropology* 34(3):281-288.

Goodman, A.H. and G.J. Armelagos. 1985a. The Chronological Distribution of Enamel Hypoplasias: A Comparison of Permanent Incisor and Canine Patterns. *Archives of Oral Biology* 30:503-507.

Goodman, A.H. and G.J. Armelagos. 1985b. Factors Affecting the Distribution of Enamel Hypoplasias within the Human Permanent Dentition. *American Journal of Physical Anthropology* 68:479-93.

Goodman, A.H., Armelagos, G.J. and J.C. Rose. 1984a. The Chronological Distribution of Enamel Hypoplasias from Prehistoric Dickson Mounds Populations. *American Journal of Physical Anthropology* 65:259-66.

Goodman, A.H., Martin, D.L. and G.J. Armelagos. 1984b. Indications of Stress from bones and Teeth, In: Cohen, M.N. and G.J. Armelagos (eds.), *Palaeopathology at the Origins of Agriculture*. pp. 13-49. Orlando: Academic Press Inc.

Goodman, A.H., L.H. Allen, G.P. Hernandez, A. Amador, L.V. Arriola, A. Chavez and G.H. Pelto. 1987. Prevelance and Age at Development of Enamel Hypoplasias in Mexican Children. *American Journal of Physical Anthropology* 72:7-19.

Gowlett, J.A.J. 2003. What Actually was the Stone Age Diet? *Journal of Nutritional & Environmental Medicine* 13(3): 143-147, DOI: 10.1080/13590840310001619338

Hengen, O.P. 1971. Cribra Orbitalia: pathogenesis and probable etiology. *Homo* 22:57-75.

Hillson, S.W. 1979. Diet and Dental Disease. *World Archaeology* 11(2):147-62.

Hurtado, A.M., Frey, M., Hurtado, I., and J. Baker. 2008. The Role of helminthes in human evolution. In: Elton, S. and P. O'Higgins (eds.), *Medicine and Evolution: Current Applications, Future Prospects*. Pp. 83—97. Florida: Boca Raton CRC.

Jacobs, K. 1993. Human postcranial variation in the Ukrainian Mesolithic-Neolithic. *Current Anthropology* 34:311-24.

Kent, S. 1986. 'The Influence of Sedentism and Aggregation on Porotic Hyperostosis and Anaemia: A case study'. *Man* (N.S.) 21:605-36.

Khotinsky, N.A. 1984. Holocene Vegetation History. In: Wright, H.E. and C.W. Barnosky (eds.), *Late Quaternary Environments of the Soviet Union*. pp. 179-200. Minneapolis: University of Minnesota Press.

Klepinger, L.L. 1992. Innovative Approaches to the Study of Past Human Health and Subsistence Strategies, In Saunders, S.R., and M.A. Katzenberg (eds.) *Skeletal Biology of Past Peoples: Research methods*. New York: Wiley Liss. pp. 121-30.

Kobashi, T., Severinghaus, J.P., Brook, E.J., Barnola, J-M. and A.M. Grachev. 2007. Precise timing and characterization of abrupt climate change 8200 years ago from air trapped in polar ice. *Quaternary Science Reviews* 26:1212-1222.

Kotova, N. and S. Makhortykh. 2010. Human adaptation to past climate changes in the northern Pontic steppe. *Quaternary International* 220(1-2):88-94.

Kremenettski, C.V. 1995. Holocene vegetation and climate history of southwestern Ukraine. *Review of Palaeobotany and Palynology* 85:289-301.

Larsson, L., Nilsson Stutz, L., Zagorska, I., Bērziņš, V. and A. Ceriņa. 2017. New Aspects of the Mesolithic—Neolithic Cemeteries and Settlement at Zvejnieki, Northern Latvia. *Acta Archaeologica* 88(1): 57-93.

Lillie, M.C. 1998a. *The Dnieper Rapids region of Ukraine: a consideration of chronology, dental pathology and diet at the Mesolithic-Neolithic transition*. Unpublished PhD thesis, Sheffield University,

Lillie, M.C., 1998b. Cranial surgery dates back to Mesolithic. *Nature* 391:854.

Lillie, M.C. 2015. *Hunters, Fishers and Foragers in Wales: Towards a social narrative of Mesolithic lifeways*. Oxford: Oxbow Books Ltd.

Lillie, M.C. 2020. Palaeopathology of the Prehistoric Populations of Ukraine, In: Lillie, M.C. and I.D. Potekhina (eds.). *Prehistoric Ukraine: From the First Hunters to the First Farmers*. pp. 235-282. Oxford: Oxbow Books.

Lillie, M.C. and M.P. Richards. 2000. Stable Isotope Analysis and Dental Evidence of Diet at the Mesolithic-Neolithic Transition in Ukraine. *Journal of Archaeological Science* 27:965-72.

Lillie, M.C. and K. Jacobs. 2006. Stable isotope analysis of fourteen individuals from the Mesolithic cemetery of Vasilyevka II, Dnieper Rapids region, Ukraine. *Journal of Archaeological Science* 33:880-886.

Lillie, M.C., Richards, M.P. and K. Jacobs. 2003. Stable Isotope Analysis of Twenty-one Individuals from the Epipalaeolithic Cemetery of Vasilyevka III, Dnieper Rapids region, Ukraine. *Journal of Archaeological Science*. 30:743-52.

Lillie, M.C., Budd, C.E., Potekhina, I.D. and R.E.M. Hedges. 2009. The Radiocarbon Reservoir Effect: New Evidence from the Cemeteries of the Middle and Lower Dnieper Basin, Ukraine. *Journal of Archaeological Science* 36:256-64.

Lillie, M.C, Budd, C. and I.D. Potekhina. 2011. Stable isotope analysis of prehistoric populations from the cemeteries of the Middle and Lower Dnieper Basin, Ukraine. *Journal of Archaeological Science* 38(1):57-68.

Lillie, M.C., Budd, C. and I.D. Potekhina. 2020. Radiocarbon dating of sites in the Dnieper Region and western Ukraine, In: Lillie, M.C. and I.D. Potekhina (eds.). *Prehistoric Ukraine: From the First Hunters to the First Farmers*. Oxford: Oxbow Books Ltd. pp. 187-233. ISBN: 9781789254587.

Macchiarelli, R. 1989. 'Prehistoric "Fish-Eaters" Along the Eastern Arabian Coasts: Dental variation, morphology, and oral health in the Ra's al-Hamra community (Qurum, Sultanate of Oman, 5th-4th Millennia BCE)'. *American Journal of Physical Anthropology* 78:575-94.

Mathieson, I., Alpaslan-Roodenberg, S., Posth, C., Szécsényi-Nagy, A., Rohland, N., Mallick, S., Olalde, I., Broomandkhoshbacht, N., Candilio, F., Cheronet, O., Fernandes, D., Ferry, M., Gamarra, B., González Fortes, G., Haak, W., Harney, E., Jones, E., Keating, D., Krause-Kyora, B., Kucukkalipci, I., Michel, M., Mittnik, A., Nägele, K., Novak, M., Oppenheimer, J., Patterson, N., Pfrengle, S., Sirak, K., Stewardson, K., Vai, S., Alexandrov, S., Alt, K.W., Andreescu, R., Antonović, D., Ash, A., Atanassova, N., Bacvarov, K., Balázs Gusztáv, M., Bocherens, H., Bolus, M., Boroneant, A., Boyadzhiev, Y., Budnik, A., Burmaz, J., Chohadzhiev, S., Conard, N.J., Cottiaux, R., Čuka, M., Cupillard, C., Drucker, D.G., Elenski, N., Francken, M., Galabova, B., Ganetsovski, G., Gély, B., Hajdu, T., Handzhyiska, V., Harvati, K., Higham, T., Iliev, S., Janković, I., Karavanić, I., Kennett, D.J., Komšo, D., Kozak, A., Labuda, D., Lari, M., Lazar, C., Leppek, M., Leshtakov, K., Lo Vetro, D., Los, Ivaylo Lozanov, D., Malina, M., Martini, F., McSweeney, K., Meller, H., Mendušić, M., Mirea, P., Moiseyev, V., Petrova, V., Price, T.D., Simalcsik, A., Sineo, L., Šlaus, M., Slavchev, V., Stanev, P., Starović, A., Szeniczey, T., Talamo, S., Teschler—Nicola, M., Thevenet, C., Valchev, I., Valentin, F., Vasilyev, S., Veljanovska, F., Venelinova, S., Veselovskaya, E., Viola, B., Virag, C., Zaninović, J., Zäuner, S., Stockhammer, P.W., Catalano, G., Krauß, R., Caramelli, D., Zariņa, G., Gaydarska, B., Lillie, M.C., Nikitin, A.G., Potekhina, I.D., Papathanasiou, A., Borić, D., Bonsall, C., Krause, J., Pinhasi R. & D. Reich. 2018. The Genomic History of Southeastern Europe. *Nature* 555:197-203. https://doi.org/10.1038/nature25778

Meiklejohn, C. and M. Zvelebil. 1991. Health status of European populations at the agricultural transition and the implications for the adoption of farming. In: Bush, H. and M. Zvelebil (eds.), *Health in Past Societies: biocultural interpretations of human skeletal remains in archaeological contexts*. pp. 129-144. Oxford: British Archaeological Reports S567.

Motuzaite Matuzeviciute, G. 2020. The adoption of agriculture: archaeobotanical studies and the earliest evidence for domesticated plants, In: Lillie, M.C. and I.D. Potekhina (eds.). *Prehistoric Ukraine: From the First Hunters to the First Farmers*. pp. 309-325. Oxford: Oxbow Books.

Nikitin, A. 2020. The Genetic Landscape of Ukraine from the Early Holocene to the Early Metal Ages, In: Lillie, M.C. and I.D. Potekhina (eds.). *Prehistoric Ukraine: From the First Hunters to the First Farmers*. pp. 327-339. Oxford: Oxbow Books.

Nuzhnyi, D. 1989. L'utilisation des Microlithes Géométriques et Non Géométriques Comme Armatures de Projectiles. *Bulletin de la Société Préhistorique Française* 86:88-96.

Nuzhnyi, D. 1990. Projectile Damage on Upper Palaeolithic Microliths and the Use of the Bow and Arrow Among Pleistocene Hunters in the Ukraine. *Proceedings. of the International Conference on Lithic Use-wear Analysis*. Sweden: Uppsala. pp. 113-24.

Pletterbauer F., Melcher A., and W. Graf. 2018. Climate Change Impacts in Riverine Ecosystems. In: Schmutz S. and J. Sendzimir (eds), *Riverine Ecosystem Management*. pp. 203-223. Springer Open: Aquatic Ecology Series, vol 8.

Potts, R. 1998. Variability selection in hominid evolution. *Evolutionary Anthropology* 7:81-96.

Revedin, A., Aranguren, B., Becattini, R., Longo, L., Marconi, E., Lippi, M. M. and J. Svoboda. 2010. Thirty thousand-year-old evidence of plant food processing. *Proceedings of the National Academy of Sciences of the United States of America* 107:18815–18819. http://doi.org/10.1073/pnas.1006993107

Roberts CA 2015 What did agriculture do for us? The bioarchaeology of health and diet. In: G Barker and C Goucher (eds): *The Cambridge World History. Volume 2: A world with agriculture, 12,000* BCE-*500 CE*. Cambridge, University Press, pp. 93-123.

Roffet-alque, M., Marciniak, A., Valdes, P.J., Pawłowska, K., Pyzel, J., Czerniak, L., Krüger, M., Roberts, C.N., Pitter, S. and R.P. Evershed. 2018. Evidence for the impact of the 8.2-kyBP climate event on Near Eastern early farmers. *Proceedings of the National Academy of Sciences* 115(35):8705-8709.

Seow, W.K. 1997. Clinical diagnosis of enamel defects: Pitfalls and practical guidelines. *International Dental Journal* 47:173-82.

Seow, W.K. 2014. Developmental defects of enamel and dentine: challenges for basic science research and clinical management. *Australian Dental Journal* 59(1 Suppl):143-54.

Stiner, M.C. 2001. Thirty years on the “Broad Spectrum Revolution” and Paleolithic demography. *Proceedings of the National Academy of Sciences* 98: 6993-6996; DOI: 10.1073/pnas.121176198.

Strassmann, B.I. and R.I.M. Dunbar. 1999. Human evolution and disease: putting the Stone Age in perspective. In: Stearns, S.C. (ed.), *Evolution in Health and Disease*. pp. 91-101. Oxford: Oxford University Press.

Stuart-Macadam, P. 1989. Nutritional deficiency diseases: a survey of scurvy, rickets and iron deficiency anemia. In: Iscan, M. Y. and K.A.R. Kennedy (eds.), *Reconstruction of life from the skeleton*. pp. 201-22. New York: Alan Liss.

Stuart-Macadam, P. 1991. Anaemia in Roman Britain: Poundbury Camp. In Bush, H., and M. Zvelebil (eds.) Health in Past Societies: Biocultural interpretations of human skeletal remains in archaeological contexts. Oxford: B.A.R. (Int. Ser.) 567:101-13.

Stuart-Macadam, P. 1992. Porotic Hyperostosis: A New Perspective. *American Journal of Physical Anthropology* 87:39-47.

Telegin, D.Ya., and I.D. Potekhina. 1987. *Neolithic Cemeteries and Populations in the Dnieper Basin*. Oxford: B.A.R. (Int. Ser.) 383.

Thomas, E.R., Wolff, E.W., Mulvaney, R., Steffensen, J.P., Johnsen, S.J., Arrowsmith, C., White, J.W.C., Vaughn, B. and T. Popp. 2007. The 8.2 ka event from Greenland ice cores. *Quaternary Science Reviews* 26:70-81.

Turner, B.L. and A.L. Thompson. 2013. Beyond the Paleolithic prescription: incorporating diversity and flexibility in the study of human diet evolution. *Nutrition Reviews* 71: 501–510. DOI: 10.1111/nure.12039.

Turner, B. L. and A.L. Thompson. 2014. Beyond the Paleolithic prescription: authors' reply to Commentary. Nutrition Reviews 72: 287–288. http://doi.org/10.1111/nure.12113

Ulijaszek, S.J., Mann, N. and S. Elton. 2012. *Evolving Human Nutrition: Implications for Public Health*. Cambridge, Cambridge University Press.

Velichko, A.A., Kurenkova, E.I. and P.M. Dolukhanov. 2009. Human socio-economic adaptation to environment in Late Palaeolithic, Mesolithic and Neolithic Eastern Europe. *Quaternary International* 203(1-2):1-9.

Wainwright, J. and G. Ayala. 2019. Teleconnections and environmental determinism: Was there really a climate-driven collapse at Late Neolithic Çatalhöyük? *Proceedings of the National Academy of Sciences* 116(9):3343-4.

Walker, P.L. 1986 Porotic hyperostosis in a marine-dependent Californian Indian population. *American Journal of Physical Anthropology* 69: 345-354.

Walker, P.L., Barthurst, R.R., Richman, R., Gjedrum, T. and V.A. Andrushko. 2009. The Causes of Porotic Hyperostosis and Cribra Orbitalia: A Reappraisal of the Iron-Deficiency-Anemia Hypothesis. *American Journal of Physical Anthropology* 139:109-25.

Winder, I.C., Devès, M.H., King, G.C.P., Bailey, G.N., Inglis, R.H. and Meredith-Williams, M.G. 2015. Evolution and dispersal of the genus Homo: a landscape approach. Journal of Human Evolution 87, 48-65). DOI: https://doi.org/10.1016/j.jhevol.2015.07.002

Wu, X., Zhang, C., Goldberg, P., Cohen, D., Pan, Y., Arpin, T. and O. Bar-Yosef. 2012. Early pottery at 20,000 years ago in Xianrendong Cave, China. *Science* 29:1696-1700.

Zaliznyak, L. 2020a. The Upper Palaeolithic, In: Lillie, M.C. and I.D. Potekhina (eds.). *Prehistoric Ukraine: From the First Hunters to the First Farmers*. pp. 63—85. Oxford: Oxbow Books.

Zaliznyak, L. 2020. Landscape change, human-landscape interactions and societal developments in the Mesolithic period, In: Lillie, M.C. and I.D. Potekhina (eds.). *Prehistoric Ukraine: From the First Hunters to the First Farmers*. pp. 87-110. Oxford: Oxbow Books.

Zilhão, J., Angelucci, D.E., Araújo Igreja, M., Arnold, L.J., Badal, E., Callapez, P., Cardoso, J.L., d'Errico, F., Daura, J., Demuro, M., Deschamps, M., Dupont, C., Gabriel, S., Hoffmann, D.L., Legoinha, P., Matias, H., Monge Soares, H.M., Nabais, M., Portela, P., Queffelec, A., Rodrigues, F. and P. Souto., 2020. Last Interglacial Iberian Neandertals as fisher-hunter-gatherers. Science 367: eaaz7943.

Zvelebil, M. 1994. Plant Use in the Mesolithic and its Role in the Transition to Farming. *Proceedings of the Prehistoric Society* 60(1):35-74.

Zvelebil, M. and P.M. Dolukhanov. 1991. The Transition to Farming in Eastern and Northern Europe. *Journal of World Prehistory* 5(3):233-78.