**Stable isotopes and dynamic diets: The Mesolithic-Neolithic dietary transition in terrestrial Central Europe**

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**Abstract**: Carbon and nitrogen stable isotopes (δ13C and δ15N) have made a huge contribution to understanding dietary change across the Mesolithic-Neolithic transition. One of the major findings is that marine resources were abandoned with the onset of farming in some coastal regions of Europe. This paper considers the isotopic evidence from terrestrial central Europe, asking whether there was a similar large-scale abandonment of freshwater resources in the early Neolithic. Using isotopic data from the published literature, stable isotope ratios from 66 Mesolithic burials are compared to 274 Neolithic individuals, from France, in-land Belgium and Germany. The results are then modelled via FRUITS (Food Reconstruction Using Isotopic Transferred Signals). The results suggest that despite a drop in fish consumption in the Neolithic, aquatic resources continued to form a small but significant part of the diet (*est*. 6%). Changes in plant protein consumption are argued to account for a greater proportion of the difference between the Mesolithic and Neolithic δ13C and δ15N isotope ratios. It is concluded that plants should see greater attention from interpretative approaches in the early Neolithic of central Europe to further our understanding of diet both as a social practice and subsistence activity.

**Keywords**: Mesolithic-Neolithic transition, dietary change, stable isotopes, FRUITS

**Highlights**:

* Central European Mesolithic and Neolithic stable isotope ratios are modelled via FRUITS.
* Low-level freshwater resource consumption continued into the Neolithic in central Europe.
* In the region under study, the contribution of plants to the diet may have seen the largest changes.

**1. Introduction**

Diet is simultaneously both biological and social, tied as much to worldviews and social relations as it is to the demands of supplying the body with sufficient calories for life (Miracle and Milner 2002; Schulting 2008; Bickle 2016; Sibbesson 2018). Reconstructing past diet is thus rarely the only goal of archaeological research into palaeodiet, and is often carried out as a first step in responding to broader research agendas (Bickle and Hofmann 2007). As a result, explaining diet variation often takes precedence in interpretation over the absolute make-up of the diet (Hamilton *et al*. 2013; Britton 2017). Nowhere is this more obvious than with the Mesolithic-Neolithic transition, in which dietary change is used as a proxy for the broader ecological and social changes accompanying the spread of farming. Stable isotope data in this context have thrown up controversial results, famously such as the ‘sharp shift’ from marine to terrestrial resources along the Atlantic façade of Europe (Richards *et al*. 2003). Debate at the time of publication highlighted the need to think carefully and contextually when interpreting stable isotope data (e.g. Hedges 2004; Richards and Schulting 2006), but also that the concepts used to discuss and represent diet in prehistory might not be as nuanced as we would wish to believe (Milner *et al*. 2004; Bickle 2016). Stable isotope analysis, primarily from bone, is now a regular technique in archaeology for determining past diets (Makarewicz and Sealy 2015; Britton 2017). Carbon and nitrogen isotope ratios, informing on protein sources, are most frequent, but other isotopes, such as sulphur, strontium, oxygen and hydrogen also feature, sometimes when inter-related issues of mobility and environment are investigated.

The Mesolithic-Neolithic transition in Europe marks a distinct change in human food production, typically characterised as the transition from hunting and gathering to farming. Meat from domesticated animals and consumption of cultivated plants, however, were not the only impactful changes in diet at the start of farming, with arrival of dairy products and news ways of producing, preparing and storing food also occurred. The main contribution made by stable isotope analysis to understanding this transition has been to reveal changes in dietary sources. While there remain gaps in evidence (e.g., fewer Mesolithic burials) and issues of definition (e.g., what do we mean by ‘sharp’ in the context of the Atlantic façade (Richards *et al*. 2003), did the Mesolithic or Neolithic see other quick changes in diet across their durations?), a move away from marine resources is now well established for some coastal regions at the start of the Neolithic. In comparison, the changes in dietary composition in terrestrial central European regions have been less well considered. While this is due in part to the evidence, e.g. a more limited archive of Mesolithic burials and distinct spatial differences in the location of Neolithic and Mesolithic burials, models of *how* the Neolithic transition took place have meant stable isotope data have played a muted role in considering the adoption of farming in this region. As the early central European Neolithic is thought to have arrived through migration, comparison between hunter-gatherer and farmer diets was considered irrelevant. However, recent studies have found that there was intermixing between indigenous central European groups and farmers moving from the south-east albeit in low numbers (Lipson *et al*. 2017). What this means in terms of the population size of both groups is relevant, but uncertain, and characterising dietary changes at this point in time could prove significant in increasing the resolution of our understanding of farmer-forager interactions. Even if there is minimal population exchange, it is therefore highly probable that incoming farmers met with indigenous hunter-gatherers and understanding dietary differences may provide more insight into the scale and landscapes of interaction. In short, migration does not ‘solve’ the transition to farming – it is a description of how it took place (Robb 2013) — we are still set the challenge of understanding the patterns and interactions of the spread of the Neolithic, of which diet was a significant element. This paper explores the contribution stable isotope studies have made to understanding the Mesolithic-Neolithic transition in Europe as a change in dietary composition, taking the transition in terrestrial central Europe as a case study and modelling changes in diet using FRUITS (Food Reconstruction Using Isotopic Transferred Signals; vβ2.1.1 Fernandes *et al*. 2014).

**2. Contribution of Stable Isotopes to Palaeodiet**

As many reviews of stable isotope analysis are now available (e.g. Makarewicz and Sealy 2015; Britton 2017), only the key points will be highlighted here and those relevant to the discussion below. The basic premise of stable isotope analysis is that the diet is the source for the consumer’s body, synthesised in body tissue as it grows, is repaired and remodelled over life. With some minor changes due to metabolism, tissues such as bone, teeth and hair thus represent the isotopic composition of the diet (DeNiro and Epstein 1978; 1981). There have been major advances in understanding the relationship between diet and consumer isotope ratios (e.g. trophic level effects; Hedges and Reynard 2007; O’Connell *et al*. 2012), but some bodily processes and conditions of production, such as manuring cereal crops, may complicate these models further (Fraser *et al*. 2011). For the most part, stable isotopes represent dietary protein consumption, but in low-protein diets, stable carbon isotopes may also represent contributions from lipids and carbohydrates (Schulting 2018). Stable isotopes represent an average isotope ratio of the dietary protein over the duration of bone turn-over, often estimated to be between 10 and 20 years. The period of bone turn-over can vary between skeletal element and over age, as well as responding to factors which effect physiological processes, such as pregnancy and starvation (Hamilton *et al*. 2013, 31). For this reason, the preference in archaeology is to compare averages between populations or groups, rather than between individuals.

The most common stable isotopes in archaeology are carbon (13C/12C) and nitrogen (15N/14N), which arise from both the plants and animals consumed. These ratios are expressed as δ13C and δ15N (the isotope ratio compared to an international agreed standard; Hamilton *et al*. 2013, 30). Stable carbon isotope ratios arising from plants in the diet vary with photosynthesis (O’Leary 1988). The largest variation is derived from consumption of ‘C3’ (temperate) and ‘C4’ (largely tropical) plants (O’Leary 1988). C3 plants from marine environments have higher δ13C isotope ratios than those from terrestrial contexts due to the ocean having a larger carbon pool than the atmosphere (Boutton 1991), and more subtle variations in δ13C have been shown to arise through the impact of canopy cover on photosynthesis (Lynch *et al*. 2008). Nitrogen isotope ratios may also be influenced by plant consumption, particularly if intensive manuring is taking place (Fraser *et al*. 2011; see below), but generally vary with the trophic level of the consumer (Hedges and Reynard 2007). Trophic level effect increases through the food chain, with 3–5‰ enrichment in nitrogen and *c*.0.5–1.5‰ in carbon proposed (Hedges and Reynard 2007; Hamilton *et al*. 2013; O’Connell *et al*. 2012;Fernandes *et al*. 2014; but see discussion in section 4.3 below). The parts per mill enrichment in nitrogen isotope ratios between the dietary protein consumed and the consumer is influenced by the amount of protein in the diet, which can be determined from the remains of the animals and plants eaten (Hedges and Reynard 2007). A larger difference between the nitrogen isotope ratios of consumer and dietary source, would indicate that humans were consuming more meat or dairy (which are indistinguishable isotopically in bone collagen). Together, therefore, the carbon and nitrogen isotope ratios of humans, and the animals and plants they were consuming, are powerful tools for reconstructing the composition of prehistoric diets.

Overall, stable isotope data have confirmed that Neolithic diets in Europe were largely terrestrial and based on C3 plants for the most part, with some possible C4 millet towards the eastern distribution (Hunt *et al*. 2008). The relative importance of animal and plant protein in forming trophic level enrichment remains a matter of debate (summarised by Dürrwächter *et al*. 2006). Earlier isotope studies have suggested significant animal protein of 60–80% for prehistoric diets, which is high when compared to modern diets from various contexts, with consumption of freshwater fish, physiological changes and differences in herbivores all suggested as possible complicating factors (Hedges and Reynard 2007, 1249). The contribution of different dietary sources made to the human stable isotope data can be modelled, using stable isotopic ratio averages from possible food sources and the expected isotope enrichments from the food chain and metabolism, to determine which mixture of dietary elements produces the closest stable isotope ratios to those of the human averages (Hedges *et al*. 2013, 364). There are often large uncertainties in both enrichment and the isotope ratios of food sources, which are greater than the instrumental errors (Fernandes *et al*. 2014). The assumption underlying these models is that humans and animals were feeding on the same plants, and hence plants would have contributed identical isotopic ratios to both animal protein and the humans who consumed both plants and the animal protein (Bogaard *et al*. 2007; Fraser *et al*. 2011; 2013). Fraser *et al*. (2011) demonstrated that manured plants would be enriched relative to non-manured plants, and further isotopic analysis of cereal and pulse remains at the early Neolithic Linearbandkeramik (LBK) site of Vaihingen, supported a dietary model where cultivated plants provided most of the dietary protein to humans (Fraser *et al*. 2013). As N2-fixing plants, with little isotopic fractionation, pulses are likely to have a δ15N close to 0‰, with manuring having significantly less impact on their nitrogen isotope ratios than on cereals, which can see an increase of *c.*6‰ or higher (Fraser *et al*. 2011). If long-term manuring of intensively managed ‘garden’-like plots of land did raise the δ15N isotope ratios of cereals (and to a lesser extent pulses), this is significant for considering many different periods through time, and particularly so for considering the Mesolithic-Neolithic transition, as manuring and cultivation may have coevally begun.

However, to date, most academic attention has fallen on the stable isotope results from the Atlantic façade (which demonstrated an immediate and almost complete abandonment of marine foods at the onset of the Neolithic and a narrowing of isotope ranges; summarised in Schulting 2015; 2018), rather than on changes in the overall composition of the diet. Did, then, the onset of the Neolithic mean a change in the proportions different foodstuffs contributed to the diet? This has important implications for how we characterise the significance of diet in shaping the transition to farming. The challenge remains to determine what the significant changes were, not only in terms of food production, but also in the proportion contribution of different foodstuffs to the diet; and this means characterising the diversity of practices in both the Mesolithic and the Neolithic. Recently, Bayesian mixing models have been developed which allow for the incorporation of multiple sources of uncertainty (Fernandes *et al*. 2014). Developed by Fernandes *et al*. (2014), FRUITS (Food Reconstruction Using Isotopic Transferred Signals) uses Bayesian mixing models of known priors (consumer stable isotope ratios, diet-consumer off-set, and stable isotopic ratio averages from food sources) to produce an estimate of the mean percentage each food type contributed to the diet, as well as the associated errors. It should be stressed, therefore, that reliability of models produced by FRUITS are entirely based on the parameters selected, and changing the parameters will change the output of the model. FRUITS can thus help to estimate the proportion contribution different food sources made to the Mesolithic and Neolithic diets in central Europe, but its results must be handled cautiously. It is thus worth remembering Box’s (1979, 202) maxim that while ‘all models are wrong, some models are useful’. With growing understanding of the isotopes from cereals, and larger bodies of data for the both the Mesolithic and Neolithic now available, FRUITS can usefully be applied to the region under discussion here for the first time.

**3. Mesolithic-Neolithic dietary transition in central Europe**

The geographical range of this paper is defined by the distribution of the Linearbandkeramik (LBK; 5500–5000 cal BC; Bickle and Whittle 2013). The Neolithic in this region began on the Great Hungarian Plain and then spread out across central Europe, eventually stretching for some 800 or more miles from the Paris basin in the west to Dneiper basin in the east. Recent aDNA analysis suggests that this distribution was mainly achieved by an expansion of population from earlier Neolithic Starčevo and Körös cultures to the south-east, with highly restricted admixture of 4-5% from indigenous groups (Lipson *et al*. 2017). However, across the distribution of the LBK there remains debated evidence for the incorporation of hunter-gatherers, in the use of cereals, lithics and pottery prior to the arrival of the LBK. The evidence for cereal growing prior to the LBK is the least certain being limited to the presence of pollen, the interpretation of which is debated and they may be large wild grasses (Behre 2007). Pollen grains in themselves do not confirm farming was taking place, but they may suggest that cereal-like plants were familiar to the late Mesolithic population. Lithic tool assemblages at LBK sites suggest continuity from the late Mesolithic, both in sources for raw material and production technique (the direct percussion for regular blades; Mateiciucová 2008, 78). Ceramics, of non-LBK origin, are also present at some early LBK sites in the western distribution. Two ceramic forms in particular, La Hoguette and Limburg, are often proposed as made by indigenous groups, and in the case of La Hoguette, found at a very small number of non-LBK sites (Manen and Mazurié de Keroualin 2003). At one of these sites, Stuttgart-Bad Cannstatt, domestic sheep/goat were found alongside red and roe deer, auroches and wild boar (Meurers-Balke and Kalis 2001). This evidence suggests some complexity of mixing between different groups, challenging the neat categorisation of diet into separate ‘hunter-gatherer’ and ‘farmer’ foods and practices.

This challenge to neat categorisation of farmers and foragers into two dietary groups, also applies to the periods of Mesolithic and Neolithic, the definition of which can vary depending on location and through time (Bickle and Hofmann 2007; Schulting 2011; 2018). Of relevance to this paper, is the extent to which different practices for procuring food extend through to different dietary compositions (both in terms of what is eaten and changing proportions of food sources). The one element of diet which has, at least elsewhere in Europe, been shown to divide Mesolithic and Neolithic diets has been the consumption of marine resources. This is complex, however, and varies across Europe. For example, the Pitted Ware culture of southern Scandinavia is classified as Middle Neolithic on the presence of ceramics, but is a mainly hunter-gatherer economy relying on seals, while the neighbouring Funnel Beaker groups (TRB), who were farmers have more terrestrial isotope ratios (Eriksson 2004; Eriksson *et al*. 2008). High resolution sampling of tooth dentine, which forms in childhood, of individuals from Neolithic Shetland found short-term episodes of high marine consumption amongst farmers, perhaps a response to times when terrestrial resources in this marginal landscape were short (Montgomery *et al*. 2013). Away from the coasts, estimating freshwater fish consumption has seen less attention than marine, but has been examined through Sulphur isotope analysis. Sulphur isotope analysis has been carried out in the Danube Gorges and at some sites in central Germany. In the Danube Gorges, where farming replaced hunting and gathering at the onset of the Neolithic, the δ34S ratios demonstrated that consumption of freshwater resources was not static across the Mesolithic or the Neolithic, and perhaps showed greater intra-site variation than chronological change (Nehlich *et al*. 2010). Stable isotopes from human remains near the Dnieper Rapids, Ukraine, demonstrate a drop in freshwater fish consumption (albeit not a total abandonment; Lille *et al*. 2009) in a context where the Neolithic is defined by the introduction of ceramics rather than a large influx of domesticates

The consumption of freshwater resources in the central Europe-LBK area remains uncertain and the evidence from stable isotopes is yet to be fully considered. Exploitation of freshwater animals such as fish, waterfowl or even turtle may have continued across the transition (Lüning 2000; Willms 2003) and archaeological evidence points to continued fishing being practiced, though much variability. Low frequency of sieving and flotation will mean under-representation, but fish bone is rarely found in any great frequency in LBK contexts (summarised in Bickle and Whittle 2013, 15–16). Exceptions are, however, to be found in the western distribution of the LBK, at sites in Belgium, the Paris basin and southern Baden-Württemberg (Lüning 2000, 153; Clavel and Arbogast 2007). In their analysis of the finds from three sites in the Oise valley, Paris basin, Clavel and Arbogast (2007, 86) found a wide variety of species, including tench, bream, rudd, chub, roach, gudgeon, pike, perch and eel in differing frequencies. These species represent a variety of fishing techniques, but could have all been fished near to the settlement (Clavel and Arbogast 2007, 87). In southern Baden-Württemberg, a possible ‘fishing station’ is identified at Lautereck, a rock shelter site with earlier LBK ceramic sherds, while at the settlement site of Singen, just north of lake Constance, a similar range of species and fishing techniques to those found in the river Oise are demonstrated (Aufdermauer *et al*. 1985, 53;Lüning 2000, 154). The range of fish skeletal parts found indicate scaling and gutting activities, likely to signal preparation for consumption (Clavel and Arbogast 2007, 87). This would suggest that LBK groups were eating freshwater resources.

Mesolithic diet in this region of Europe seems to have broadly relied on terrestrial hunted wild species, such as red deer, wild boar and aurochs among others, and a large range of wild plants, including nuts, seeds and tubers, suggesting a varied diet, which could have seen distinct seasonal variation (Gronenborn 1999; Jochim 1998; 2008). Fish and other freshwater resources are known from the Mesolithic sites, though their role in the diet may not have been as strong as marine resources in coastal hunter-gatherer diet. At Noyen-sur-Seine, Paris basin, human isotope signals suggested local aquatic resources were *c*.30–40% of the diet (Drucker *et al*. 2016). These resources included a variety of fish, such as pike, brown trout, burbot, cyprinid, as well as eel, pond turtle and possibly otter (Drucker *et al*. 2016). In the Meuse basin, Bocherens *et al*. (2007) suggest that the main contribution to dietary protein came from terrestrial sources, with freshwater resources a possible addition that explained variation between the humans sampled. Therefore, as for the Neolithic, assuming a monolithic ‘Mesolithic’ diet would be a mistake, and quite diverse patterns may have been the norm.

**4. Isotopes from central Europe**

Before the isotopes from the Mesolithic and Neolithic are compared, there are several important analytical and archaeological limitations to consider. Representivity of the samples are influenced by both regional and local differences in taphonomy and human activity in the past. Mesolithic human remains are found far less frequently than in the Neolithic and, in addition, we cannot assume that these burials represent the whole population, as who was buried may have been subject to some degree of social selection. Such considerations apply to the animal remains for determining the food web, as social rules and expectations around the discard of waste may have determined what is preserved. Chronological representation may also be problematic, as a cemetery or burial location may represent one event or several centuries of activity. In the case of the data analysed in this paper, uneven representation is a large issue. Mesolithic burials are stretched out over several 1000 years, whereas the Neolithic are from a 400 year period. In both cases, animal bones will not necessarily arise from the same contexts as the human burials. The data therefore need to be analysed cautiously, and as representing the relative, rather than absolute, differences between the Mesolithic and Neolithic.

*4.1 The Mesolithic and Neolithic human and animal isotope data*

The Mesolithic isotope data collected for this paper (66 burials), come from across the timespan of the Mesolithic, but are concentrated in what would become the western distribution of the LBK. About half come from in-land Belgium (29 burials), with seven burials from France, one from Luxembourg and 28 from Germany. All except one burial, have known radiocarbon dates. The δ13C isotope ratios from two of the German burials (Bad Dürrenberg and Abri Fuchskirche) are taken from published datelists, which only reported the stable carbon isotope ratio (see Appendix A). There are only three males in the dataset, 19 females, 18 unsexed adults, 25 non-adults and three instances where age and sex data was not available. For the early Neolithic data, the analyses are based on 274 Linearbandkeramik burials from the same regions as the Mesolithic data. This includes cemetery sites from Alsace, Baden-Württemburg and Bavaria (which are reported in full in Bickle and Whittle 2013, including analytical methods; see Appendix B). There are 106 females, 99 males, 18 unsexed adults, 47 non-adults and four individuals for whom neither sex nor gender could be identified.

The aim of the analysis is to determine the extent of change in stable nitrogen and carbon isotope ratios as a proxy for how the *content* of the diet (as identifiable through stable isotopes) changed in terms of the proportion of food stuffs, with a particular interest in freshwater resource consumption. From the Mesolithic, terrestrial and aquatic animal bone data were available from the Paris Basin, the Meuse Basin and Luxembourg (see Appendix C); from the Neolithic, faunal data from Bickle and Whittle (2013) were supplemented with four fish stable isotope ratios from Herxheim (Dürrwächter *et al*. 2006; Appendix D).

*4.2 Results*

The mean ratios from the human carbon and nitrogen isotopes are reported in tables 1 and 2 and figures 1 and 2. Detailed data, including the available quality indicators, are reported in the supplementary material. For the Mesolithic human data, carbon isotope ratios range from -16.9‰ to -21.8‰, with a mean of -20.3‰±0.60 for all adults and -20.1‰±0.74 for all data. Mesolithic human nitrogen isotope ratios range from 8.4‰ to 13.8‰, with a mean of 10.1‰±0.92 for all adults and 10.5‰±1.04 for all data. For the Neolithic human data, carbon isotope ratios range from -19.6‰ to -21.0‰, with a mean of -20.2‰±0.27 for all adults and -20.2‰±0.26 for all data. Neolithic human nitrogen isotope ratios range from 7.6‰ to 11.7‰, with a mean of 9.4‰±0.78 for all adults and 9.4‰±0.84 for all data. The means of the Mesolithic and Neolithic nitrogen stable isotope ratios for all adults are statistically different (p<0.001, 2-tailed *t*-test assuming unequal variances), but not for carbon, where the difference is only of 0.1‰. The variation in nitrogen stable isotope ratios for all adults is also statically different (Mann-Whitney U test, p<0.001), but again not for carbon. These results confirm the expectation that there was less variation in meat protein consumption in the Neolithic than in the Mesolithic diets, though not to the extent found in other regions of Europe (Schulting 2015).

*Table 1: Average values for the human δ13C and δ15N isotope ratios for the Mesolithic. N values for δ13C and δ15N are reported separately, because δ15N is not known for 2 individuals.*

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | **Mean δ13C** | **SD δ13C** | **Mean δ15N** | **SD δ15N** | **n δ13C** | **n δ15N** |
| All Adults | -20.3 | 0.60 | 10.1 | 0.92 | 40 | 39 |
| Female | -20.0 | 0.37 | 10.1 | 0.65 | 19 | 18 |
| Male | -20.0 | 0.47 | 11.1 | 0.68 | 3 | 3 |
| Non-Adult | -19.8 | 0.95 | 10.0 | 1.09 | 23 | 22 |
| All data | -20.1 | 0.74 | 10.5 | 1.04 | 66 | 64 |

*Table 2: Average values for the human δ13C and δ15N isotope ratios for the Neolithic.*

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | **Mean δ13C** | **SD δ13C** | **Mean δ15N** | **SD δ15N** | **n δ13C** |
| All Adults | -20.2 | 0.27 | 9.4 | 0.78 | 223 |
| Female | -20.3 | 0.23 | 9.3 | 0.77 | 106 |
| Male | -20.2 | 0.27 | 9.5 | 0.73 | 99 |
| Non-adult | -20.3 | 0.22 | 9.3 | 1.06 | 47 |
| All data | -20.2 | 0.26 | 9.4 | 0.84 | 274 |

The mean stable isotope ratios from the animal data are reported in tables 3 and 4, with mean ratios shown in figures 1 and 2. The Mesolithic terrestrial (T) and aquatic (A) animals have approximately the same average δ13C isotope ratios (T=-22.4‰±2.14; A=-22.0‰±1.49), and, as expected, aquatic animals have a much higher δ15N average ratio than terrestrial species (T=6.9‰±2.26; A=9.5‰±1.45). Neolithic terrestrial and aquatic animals also have similar average δ13C isotope ratios (T=-21.3‰±1.06 and A=-21.5‰±1) and are closer in their average nitrogen isotope ratios than in the Mesolithic (T=6.7‰±1.4 and A=8.9‰±1.1). Although low numbers of aquatic resources from the Neolithic (n=4) urges caution in interpreting patterns in the data, there are no statistical differences in the Mesolithic and Neolithic aquatic animal isotope ratios (2-tailed *t*-test). However,Neolithic terrestrial animals have statistically significantly different δ13C and δ15N ratios (p=0.002 and p=0.003 respectively, 2-tailed *t*-test assuming unequal variances) to the terrestrial animals dating to the Mesolithic. This may be due to where domestic animals were kept or herded, what they fed on and the type of terrestrial animals in the human diet (e.g. less canopy cover, fodder from open environments, and fewer omnivores in the diet).

*Table 3: Average values for the animal δ13C and δ15N isotope ratios for the Mesolithic.*

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Species** | **Mean δ13C** | **SD δ13C** | **Mean δ15N** | **SD δ15N** | **n** |
| Aurochs | -23.1 | 0.38 | 5.5 | 0.48 | 6 |
| Brown Trout | -19.9 | 0.74 | 9 | 0.32 | 5 |
| Burbot | -23.2 | 1.02 | 8.7 | 1.81 | 4 |
| Cyprinidae | -21.8 | 0.4 | 10.1 | 1.39 | 5 |
| Eel | -23.8 |  | 8.3 |  | 1 |
| Lynx | -19.1 |  | 11.9 |  | 1 |
| Nase | -20.1 |  | 8.7 |  | 1 |
| Otter | -22.5 | 2.75 | 11.4 | 0.83 | 3 |
| Pike | -22.1 | 1.35 | 10 | 1.27 | 4 |
| Pond Turtle | -25.8 | 0.7 | 7.8 | 0.39 | 4 |
| Red Deer | -22.8 | 0.29 | 5.8 | 1.5 | 6 |
| Red Fox | -21.2 |  | 12.4 |  | 1 |
| Roe Deer | -23.3 | 0.29 | 5.8 | 1.5 | 6 |
| Wild Boar | -20.3 | 0.87 | 7 | 1.43 | 7 |
| Wild Cat | -19.8 |  | 9.3 |  | 1 |
| Wolf | -21.3 |  | 9.3 |  | 1 |

*Table 4: Average values for the animal δ13C and δ15N isotope ratios for the Neolithic.*

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Species** | **Mean δ13C** | **SD δ13C** | **Mean δ15N** | **SD δ15N** | **n** |
| Cattle | -21.7 | 1.17 | 6.5 | 1.48 | 57 |
| Goat | -19.8 | 0.64 | 6.5 | 2.01 | 2 |
| Pig | -20.7 | 0.27 | 7.2 | 1.21 | 21 |
| Sheep/goat | -20.7 | 0.51 | 6.9 | 1.38 | 20 |
| Fish | -21.5 | 1.0 | 8.9 | 1.1 | 4 |



*Figure 1: The Mesolithic human isotope data, and averages for the animal isotope data, expressed as mean and SD.*



*Figure 2: The Neolithic human isotope data, and averages for the animal isotope data, expressed as mean and SD. Note scales are the same as for Figure 2 for comparison.*

*4.3 Modelling the dietary change*

The relative contribution of different dietary sources was modelled using the Bayesian mixing model FRUITS (Food Reconstruction Using Isotopic Transferred Signals; vβ2.1.1 Fernandes *et al*. 2014). The consumer targets, food sources, and off-set values used are reported in table 5. Some of the source isotope ratios are not known and had to be estimated from the literature, particularly those for plants, where the extent and consistency in manuring is uncertain. Plants for the Mesolithic, were estimate based on discussion in Hedges *et al*. (2013, 363–5), and for the Neolithic, from the isotopic analysis of the cereals from the LBK site of Vaihingen (Fraser *et al*. 2013).Values for off-sets (based on the assumption that humans “are what they eat + X‰”) introduce uncertainty in the model, as they are not known for certain, particularly for the enrichment in nitrogen isotope ratios between food source and consumer (Hedges and Reynard 2007; O’Connell *et al*.2012). The danger in underestimating the nitrogen off-set is that the proportion of protein in the diet arising from animals will be overestimated (O’Connell *et al*. 2012, 432; see also Styring *et al*. 2015; the reverse will also be true). For this reason, an off-set of +6‰ was used following O’Connell *et al*. (2012) and Denaire *et al*. (2017), and will provide a different model of the diet to Hedges *et al*. (2013), which modelled the LBK diet based on a δ15Noff-set of +4–4.5‰. It is worth emphasising again that the output of the model is contingent on the input parameters. The inputs used here are therefore judged to be most likely, but will be refined by future research.

*Table 5: Summary input parameters for FRUITS model. The average isotope ratios for the human data are all adults (from tables 1 and 2), to avoid breastfeeding signal from infants.*

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Mean δ13C** | **SD δ13C** | **Mean δ15N** | **SD δ15N** |
| **Mesolithic** |  | | | |
| Human | -20.3 | 0.6 | 10.1 | 0.92 |
| Terrestrial | -22.4 | 2.14 | 6.9 | 2.26 |
| Aquatic | -22.0 | 1.49 | 9.3 | 1.44 |
| Plants | -24.8 | 1.06 | 1.5 | 1.5 |
| Off-sets | 4.8 | 0.2 | 6 | 0.5 |
| **Neolithic** |  | | | |
| Human | -20.2 | 0.27 | 9.4 | 0.78 |
| Terrestrial | -21.3 | 1.06 | 6.7 | 1.4 |
| Aquatic | -21.5 | 1 | 8.9 | 1.1 |
| Plants | -23.8 | 0.3 | 3.6 | 1.2 |
| Off-sets | 4.8 | 0.2 | 6 | 0.5 |

The main question asked of the analysis was whether any inference could be made about changes in freshwater reource consumption, with a hypothesis that there was a decrease from the Mesolithic to the Neolithic. However, there are several other variables that complicate the analysis. Namely, (1) the percentage of meat vs. milk in the diet is unknown, (2) the impact of manuring on the cereal isotopes ratios, as this may not be consistent across the distribution of sites during the Neolithic, (3) the extent of pulses in the diet. As these variables show, the input parameters are not likely to be an absolute representation of the diet, but these models should give some insights into the dietary changes in terms of relative proportion contribution of foodstuffs between the Mesolithic and Neolithic.

The results of the FRUITS modelling are reported in table 6 and figures 3 and 4. The models suggest that the contribution of aquatic animals to the diet fell from *c*.18.5±13.8% in the Mesolithic to *c*.5.9±6.8% in the Neolithic (note the large standard deviations). This suggests a significant drop, but not a complete abandonment of aquatic resources between the Mesolithic and Neolithic in terrestrial areas of central Europe. In contrast to previous models, the analysis presented here suggests that the contribution of plant protein to the diet has previously been underestimated in the Neolithic (the model suggesting plants accounted for nearly 84.3±17.6% of the protein in the diet). This is a higher percentage of the diet than was suggested at sites where the plant isotope ratios were taken from (Fraser *et al*.2013). This may suggest that manuring may not have been consistent across the LBK. At sites with less established cereal growing and manuring than Vaihingen, the off-set would be lower, and, hence, leading to plants being overestimated in the model. It is likely, however, that the contribution of plants to dietary protein to the LBK-Neolithic diet has previously been underestimated. Hedges *et al*. (2013, 365), concluded that in the geographic region under study here, at +4‰ enrichment the LBK diet was likely to be 40% meat protein, 5% fish and few pulses; at closer to +4.5‰, the meat protein would have likely been higher at 50–55%. The estimation of 5% contribution from fish seems to have been a reasonable suggestion, but with the caveat that the terrestrial contribution could have been higher if the manuring of crops was not widespread (see also Denaire *et al*. 2017). Even reducing both the trophic level off-set and the δ13C and δ15N isotope ratios to more conservative estimates, FRUITS models still suggest that plant protein made up *c*.60% of the overall dietary protein. Perhaps the most surprising element of the models are the extent to which they suggest the proportion of terrestrial animals in the diet decreases from the Mesolithic and Neolithic (a decrease of about 15% at largest estimation). Due to the time spread of the Mesolithic data, the speed of this change cannot be judged from these data. However, the models lend some weight to a hypothesis that the significant shift in diet from the Mesolithic to the Neolithic may have only minimally been associated with a decrease in use of aquatic resources in this region and rather associated with the consumption and growing conditions of plants altering the overall make-up of the diet protein.



*Figure 3: Box plot of FRUITS results for Mesolithic diet contribution from animals, fish and plants.*



*Figure 4: Box plot of FRUITS results for Neolithic diet contribution from animals, fish and plants.*

*Table 6: The results of the FRUITS model of Mesolithic and Neolithic diet*

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | **Mean** | **SD** | **2.5pc** | **Median** | **97.5pc** |
| **Mesolithic** |  |  |  |  |  |
| Terrestrial | 0.2658 | 0.2091 | 0.009817 | 0.2159 | 0.7783 |
| Aquatic | 0.185 | 0.1381 | 0.007005 | 0.1575 | 0.5136 |
| Plants | 0.5492 | 0.2008 | 0.1034 | 0.5685 | 0.8868 |
| **Neolithic** |  |  |  |  |  |
| Terrestrial | 0.09733 | 0.1677 | 0.001367 | 0.03997 | 0.7353 |
| Aquatic | 0.05948 | 0.06798 | 0.001413 | 0.0387 | 0.243 |
| Plants | 0.8432 | 0.1767 | 0.204 | 0.8994 | 0.9848 |

**5. Discussion and conclusions**

The results of the analysis and discussion above, suggest more variability in dietary protein sources in the Mesolithic when compared with the Neolithic. For the sexed burials there was a larger gap in average δ15N isotope ratios between females and males in the Mesolithic than in the Neolithic (compare tables 1 and 2; though low numbers of sexed burials in the Mesolithic urge caution in interpreting the data). The change in diet is also associated with a drop in, but not complete abandonment of, freshwater resource consumption in the central European Neolithic diet (on the basis of the FRUITS model). At the early Neolithic cemetery site of Vedrovice, Czech Republic, the population had an average δ34S isotope ratio of 0, with a range of -2 to +2 (Richards *et al*. 2008, 189), but without comparable δ34S isotope ratios from local fish it is hard to interpret the extent of freshwater resource consumption these data indicate. In central Germany, Nehlich *et al*. (2014, 22) suggest only limited freshwater fish consumption on the basis of their results from a series of Neolithic sites, though this is raised as a possibility for a series of outliers with both high δ34S and δ15N isotope ratios. The results here, in contrast, suggest that low-level fish consumption was found in the LBK. Interestingly, in Belgium, the relative contribution of aquatic resources to the total dietary protein consumed increases again in the Middle Neolithic (Bocherens *et al*. 2007), but there are no human stable isotope data from the LBK in this region, as few human remains have been preserved. It is tempting to connect the increase in aquatic resources after the LBK with the resurgence of the mitochondrial haplogroup U, which is present in pre-farming central Europe and thus identified as denoting hunter-gatherer ancestry (Bollogino 2013). This is potentially a Europe-wide phenomenon, with hunter-gatherer ancestry of the population increasing from 4-5% in the LBK to 17% in the Middle Neolithic (Lipson *et al*. 2018). During the Late Neolithic at Blätterhöle (Hagen, Germany), individuals with the U haplogroup had more aquatic resources in their diet than those with haplogroups denoting farming ancestry, in fact, the two groups had two isotopically distinct diets (Bollogino 2013, 481). In contrast, the analysis presented here suggests that central European Mesolithic and early Neolithic groups were neither exclusive populations nor ate exclusive diets. Rather, the reduction in isotopic variability with the introduction of farming may indicate that shared dietary practices were a strong part of community cohesion for early agricultural communities.

The FRUITS dietary models also suggest that the introduction of cereals may have increased the proportion of plant protein in the diet between the Mesolithic and Neolithic, lending support to Fraser *et al*.’s (2013; see also Oelze *et al*. 2011) argument that manured crops probably formed the dominant protein source in the Neolithic. This chimes with Marciniak’s (2005) proposal that animal meat was not part of the daily diet in the Neolithic, but rather consumed at intermittent feasting events (see also Bickle 2016). Overall, the analysis here suggests that the differences in *consumption* of faunal protein (both terrestrial and freshwater) between the Mesolithic and Neolithic in central Europe were less distinctive than those associated with plant protein consumption. This necessarily tentative conclusion should not be confused with changes in subsistence practices, in which the social implications of hunting versus herding or gathering versus growing could have been considerable, but these conclusions do add further detail to our understanding of Neolithic ‘foodways’ (Schulting 2008). Previous accounts of the transition in Europe, which envisaged greater continuity in the use of plant resources from the Mesolithic to the Neolithic (Zvelebil 1994, 64), could now be revisited to consider how the change from gathering to growing impacted on the role plants played in the diet. There are limitations to the FRUITS models and further isotopic analysis of plants from both the Mesolithic and Neolithic periods would benefit the reliability of the conclusions. While animals frequently play a large role in our interpretative accounts of the spread of farming and Neolithic social worlds (e.g. Whittle 2003), despite notable exceptions, plants have had a more muted role. This discussion demonstrates that how plants were managed and consumed in the Neolithic deserves further attention from both the perspective of their place in the diet and how results from their analysis can be drawn into our interpretative accounts of the Mesolithic-Neolithic transition (Saul *et al*. 2014).

**Appendices**

Appendix A: the Mesolithic human isotope data. Age and sex reported as expressed in published literature. U=undetermined.

Appendix B: the Neolithic human isotope data (all from Bickle and Whittle 2013). Age and sex reported as expressed in published literature. U=undetermined.

Appendix C: the Mesolithic animal isotope data

Appendix D: the Neolithic animal isotope data (all from Bickle and Whittle 2013, except the four fish isotope ratios, which are from Dürrwächter et al. 2006).

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