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The transition from foraging to farming (7000–500 cal BC) in the SE Baltic: a re-evaluation of chronological and palaeodietary evidence from human remains

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Abstract

Our knowledge of the timing and completeness of the transition from foraging, fishing and hunting to food production in boreal northeastern Europe is far from clear. Here, we present new bone collagen AMS 14 C dates, and δ^{13} C and δ^{15} N isotope values for 20 humans and 17 animals from a 7,500-year period dating from the Late Mesolithic to the Bronze Age in Lithuania. AMS ¹⁴C dates revealed large discrepancies in comparison to previously obtained radiocarbon dates, thus highlighting the need to re-date all prehistoric human remains where chronology was based on ¹⁴C dating of bone collagen. Stable isotope data indicate that inland Mesolithic-Subneolithic huntergatherers (7000–3000 cal BC) relied on a balance of freshwater food and game animals with regard to protein intake. The coastal Subneolithic groups (ca. 3000 cal BC) relied heavily on lagoon fishing, while seals and forest game were of lesser importance. Animal husbandry, most likely of sheep or goats, was a main source of protein for Neolithic Corded Ware Culture people (2900– 2400 cal BC), although a significant contribution of freshwater food is also evident. Significant intra-individual variation in stable isotope values may demonstrate that a highly flexible subsistence strategy was adopted by the CWC people. Unusually high δ^{13} C values indicate that millet had been already introduced into the farming economy of the Late Bronze Age around 1000 cal BC.

Keywords: AMS 14 C dates; δ^{13} C and δ^{15} N stable isotopes; diet; human remains; southeastern Baltic

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Introduction

The Neolithic transition in the boreal zone of Eastern Europe deviated significantly from the "classic" European neolithisation model, details of which are still far from being completely understood. Yet how farming became established in an environment so rich in wild foodstuffs and so much less prepossessing for crop production is an important question in European prehistory. Zooarchaeological data supports the hypothesis that mixed economies with limited animal husbandry were developed around lagoonal or inland lakes during the Neolithic (3200-2000 cal BC), and continued into the Bronze Age (Piličiauskas, 2016). ¹

The aim of the research reported here was twofold – to reconstruct a more comprehensive view of hunter-gatherers', as well as first farmers', dietary patterns and their change during the Holocene in the southeastern Baltic, and to refine the chronology of Lithuanian Stone and Bronze Age human remains. In the southeastern Baltic region there are no known large Stone or Bronze Age cemeteries akin to those in Northern Latvia, for example (Zagorskis, 2004). Human remains are instead found in small cemeteries, single graves, or as loose bones in refuse layers of ancient lakeshore settlements or fishing stations. These small cemeteries usually contain skeletons from different time periods, burial artefacts are few, and where present, their association with the burial is not guaranteed. Due to this, burial artefacts and burial customs generally cannot be used to date the burial. It is therefore essential to have direct and reliable ¹⁴C dates of almost all Stone and Bronze Age skeletons. As such, burials having suspiciously late ¹⁴C dates or large uncertainties (of ± 100 years BP and more) were re-dated here by AMS ¹⁴C, as well some graves and loose bones that had not been previously radiocarbon dated.

Another potential of human remains lies in the composition of bone collagen stable isotopic ratios of carbon (δ^{13} C) and nitrogen (δ^{15} N) which can be used to infer dietary patterns across time and/or space (Vogel and van der Merwe, 1977; DeNiro, 1987;), and also intra-individual dietary change (see Eriksson and Lidén, 2013). The ratio of ¹⁵N to ¹⁴N increases with each trophic level and it can be used to identify breastfeeding infants, and consumers of high trophic level foods, e.g. aquatic resources (Hedges and Reynard, 2007). The ¹³C to ¹²C ratio in human tissues provides an indication of the amount of freshwater and marine foods as well as C₃ and C₄ plants consumed (Richards and Hedges, 1999; Schoeninger, 2009). This approach has been extensively used to examine the magnitude of dietary change following the introduction of farming in other parts of Europe (e.g. Tauber, 1981; Richards et al., 2003; Schulting, 2011; Lelli et al., 2012). During this project all available Lithuanian human remains (n=20), including the newest discoveries, were sampled for carbon and nitrogen stable isotope analysis. In addition, prehistoric animal and fish species (n=17) were analysed for carbon and nitrogen stable isotopes. To our sample we also add the published

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¹ In this paper we use the following time periods of Lithuanian prehistory: Late Mesolithic 7000–5000 cal BC, Subneolithic 5000–2900 cal BC, Neolithic 3200/2900–2000 cal BC, Early Bronze Age 2000–1300 cal BC, and Late Bronze Age 1300–500 cal BC (Piličiauskas, 2016). The appearance of pottery shall be considered as the criterion of the beginning of the Subneolithic, and farming of the Neolithic.

Lithuanian isotopic data from 20 humans and 42 animals dating from the Stone to Bronze Ages (Antanaitis-Jacobs et al., 2009).

Sites

The human and animal bone materials analysed in this study are mainly from inland Lithuanian Mesolithic-Neolithic cemeteries (Donkalnis, Spiginas, and Kretuonas 1B), Corded Ware Culture (thereafter CWC) single graves (Gyvakarai, Biržai, and Plinkaigalis), a single Late Bronze Age (thereafter LBA) sacrificial site (Turlojiškė), as well as from refuse layers of Subneolithic-Neolithic dwelling sites (Nida, Žemaitiškė 2, Daktariškė 1, and 5) (Table 1; Fig. 1). Stable isotope data from important coastal Subneolithic-Neolithic sites at Šventoji as well as from the nearby Benaičiai cemetery are briefly discussed, although are published in detail elsewhere (Piličiauskas et al., 2017b). Many of these archaeological sites have been previously and extensively investigated (Butrimas, 1982; Butrimas et al., 1985; Rimantienė, 1989; Butrimas, 1992; Kazakevičius, 1993; Girininkas, 1994; Tebelškis and Jankauskas, 2006; Merkevičius, 2012). A recently discovered Biržai CWC grave (Duderis, 2015), as well as the Nida Subneolithic-Neolithic coastal site (3500–2400 cal BC), where new field investigations were launched by G. Piličiauskas in 2011 and which are still continuing today (for first results see Piličiauskas and Heron, 2015), are the only exceptions.

Materials and Methods

Previous to this study, 28 ¹⁴C dates were published for Lithuanian Stone Age-Bronze Age human remains (Butrimas et al., 1985; Merkevičius, 2005; Tebelškis and Jankauskas, 2006; Antanaitis-Jacobs et al., 2009; Piličiauskas and Heron, 2015; Piličiauskas et al., 2017b). For this study we attempted to date a further 16 individuals from the previously established period of 7000–500 cal BC (Table 1).

Direct AMS ¹⁴C dates of human bones and associated materials were undertaken at Poznań Radiocarbon Laboratory. We had no information about consolidants having been used for prior conservation of the skeletal material, and no traces were detected during visual inspection of the dated bone samples with the exception of a single individual from Spiginas grave 2. To remove the unknown consolidant the sample was treated with acetone and alcohol before dating. Extraction of collagen was performed using the procedures originally described by Longin (1971), with further modifications (Piotrowska and Goslar, 2002). The extracted collagen was ultrafiltered using pre-cleaned VivaspinTM 15kDa MWCO filters (Brown et al., 1988; Bronk Ramsey et al., 2004). All dates in this study were calibrated by using OxCal 4.2 software and IntCal13 atmospheric curve (Bronk Ramsey, 2009; Reimer et al., 2013). Dates are discussed with 95.4% probability when calibrated.

In total, 31 bone and dentine collagen $\delta^{13}C$ and $\delta^{15}N$ values for 20 humans, and 17 bone collagen $\delta^{13}C$ and $\delta^{15}N$ values for forest, marine and domestic animals are included in this study. Isotopic data from 16 of the 20 human individuals was previously published by Antanaitis-Jacobs et al. (2009). As such, we report here the results of repeated measurements on the same individuals as Antanaitis-Jacobs et al. (2009), as well as those made on tooth dentine which was not analysed in the previously published study. In addition we also include data from 12 humans published by Piličiauskas and colleagues (2017). In total, stable isotope values for 32 Stone and Bronze Age humans from coastal sites are used for dietary reconstruction (Antanaitis-Jacobs et al., 2009; Piličiauskas et al., 2017b). Collagen from 40 human and animal samples was extracted at the Laboratory for Bioarchaeological Research at the University of Central Florida and analysed at the Colorado Plateau Stable Isotope Laboratory at North Arizona University (NAU), and of these, eight human samples were re-analysed at the University of York (UoY) in order to understand the origin of inter-laboratory variability among the samples tested at NAU and the Max Planck Institute (MPI) (Antanaitis-Jacobs et al., 2009).

At the University of Central Florida collagen was extracted using a modified version of the Longin (1971) protocol and dentine collagen extraction followed a similar procedure as outlined by Wright and Schwarcz (1999). Bone and tooth samples were cleaned by utrasonication and then left to dry in a 60°C oven for a minimum of 12 hours. Each sample was ground into two to five millimeter fragments, and from this three to five grams of bone and all the dentine was used for extraction. Each sample was treated with 2:1 chloroform:methanol mixture to remove any remaining lipids. After drying the samples were demineralized in 0.5 M HCl, with acid changed daily until complete demineralisation was achieved. Demineralised samples were rinsed with distilled water until attaining a pH of 2.5 to 3.0. Samples were treated with 0.1 M NaOH for humic acid removal, and then rinsed with distilled water to a pH of 7.0 ± 1.0 . Samples were rinsed in 0.25 M HCl and then distilled water was added to each sample until a pH of 2.5 to 3.0 was achieved. Samples were then placed in a 90°C oven for 16 hours. Gelatinised samples were pipetted into two-dram glass vials and placed in a 90°C oven until the remaining collagen was dry. Stable isotope analysis was performed using a Thermo- Electron DELTA V Advantage isotope ratio mass spectrometer with a CONFLO III using a Carlo Erba NC2100 Elemental Analyzer. Precision of analysis was determined by completing duplicate sample analyses (10%), which for δ^{13} C was $\pm 0.09\%$, and for δ^{15} N was $\pm 0.07\%$ o. Accuracy was assessed using a laboratory standard (NIST peach leaves), which gave an average δ^{13} C value of -26.17±0.03‰, and an average δ^{15} N value of 1.67±0.01‰ for 11 analyses.

Collagen extraction at the University of York followed a modified Longin collagen extraction protocol (1971) using ultrafiltration (30kDa MWCO) on approximately 500mg of bone (Brown et al., 1988; Richards and Hedges, 1999; Colonese et al., 2015). Samples were initially cleaned manually using a scalpel, and then were demineralised in 0.6M aq. HCl solution at 4°C, and the resulting insoluble fraction gelatinised in pH3 HCl for 48h at 80°C. The supernatant solution was then ultrafiltered (30kDa MWCO, Amicon) to isolate the high molecular weight fraction, which was then lyophilised. Purified collagen samples (1mg) were analysed at the University of York in

duplicate by EA-IRMS on a Sercon GSL analyser coupled to a Sercon 20-22 Mass Spectrometer. Accuracy was determined by measurements of international standard reference materials within each analytical run. These were IAEA 600 $\delta^{13}C_{raw}$ = -27.7 ±0.1, $\delta^{13}C_{true}$ = -27.8 ±0.0, $\delta^{15}N_{raw}$ = 0.5 ±0.2, $\delta^{15}N_{true}$ = 1.0 ±0.2; IAEA N2 $\delta^{15}N_{raw}$ = 20.6 ±0.1, $\delta^{15}N_{true}$ =20.3 ±0.2; IA Cane, $\delta^{13}C_{raw}$ -11.8 ±0.1; $\delta^{13}C_{true}$ = -11.6 ±0.00. In addition, a homogenised bovine bone extracted and analysed within the same batch as the samples produced the following values; $\delta^{13}C$ = -22.9 ±0.1; $\delta^{15}N$ = 7.0 ±0.2. The overall mean value among 50 separate extracts of this bone sample produced values of $\delta^{13}C$ = -23.0 ±0.3 and $\delta^{15}N$ = 6.7 ±0.4.

In all cases, stable isotope ratios are expressed as 'per mil' or parts per thousand (‰). The difference in the 15 N/ 14 N ratio between the sample and the internationally defined standard AIR (atmospheric air) in ‰ units is referred to as δ^{15} N, and δ^{13} C refers to the difference in 13 C/ 12 C ratio between the sample and the internationally defined standard, PDB (Vienna Peedee Belemnite Limestone). The reported ratios are calculated using the equation: $\delta X = ((R_{sample} - R_{standard})/R_{standard}) \times 1000$.

Results and Discussion

Chronology of human remains

Nine of the sixteen samples were AMS dated with success, while in six cases collagen preservation was too poor, and in one case a modern date was obtained for an ungulate bone which suggests that this bone is not associated with the Mesolithic grave 3 at the Spiginas cemetery (Table 2). From the nine successfully dated samples, three of the samples had been previously dated and were included in this analysis in order to test the reliability of the previous dating results (i.e. Gyvakarai, Spiginas grave 2, and Turlojiškė grave 3).

The oldest dates in the new AMS 14 C dataset are from double grave 5 in the Donkalnis cemetery. Bones from a child and an infant were found to be of a comparable date, i.e. dating to the Late Mesolithic -7140 ± 40 BP (Poz-61589) and 7110 ± 40 BP (Poz-61588) (combined date 7125 ± 29 BP, 6060-5925 cal BC). Another burial from the same cemetery, grave 6, appears to be from a much later period, i.e. Subneolithic (5770 ± 40 BP (Poz-61574), 4720-4530 cal BC). Graves 2 and 3 from the Spiginas cemetery were re-dated by AMS. A human bone from Grave 2, previously dated by the beta decay radiocarbon method and showing a large uncertainty (4080 ± 120 BP (GIN-5570), 2910-2300 cal BC) was shown to be significantly younger with the AMS dating method (3580 ± 60 BP (Poz-61573), 2130-1750 cal BC). Grave 3 from the Spiginas cemetery was previously dated by AMS at the Oxford laboratory (7780 ± 65 BP (OxA-5925), 6800-6460 cal BC), giving the opportunity to investigate the FRE of Biržulis Lake. This was possible through the dating of an ungulate long bone labelled in the museum as part of the inventory of the grave 3. Unfortunately, the AMS 14 C date of the sample revealed it to be modern, 175 ± 30 BP (Poz-61571),

indicating that the sample was a recent deposit. This finding cautions against the uncritical acceptance of artefacts as being associated with Stone Age burials, particularly when recovered from shallow and often disturbed graves. Burials such as these may contain more recent or even modern materials that are visually indistinguishable from the original burial artefacts.

Direct AMS 14 C dates are of even greater importance when dealing with single or loose human bones from ancient dwelling or other sites. Very often these bones come from unprovenanced and poorly documented contexts. For example, we were able to date the human skull fragment from the Daktariškė 1 site to the Subneolithic period (4635 ± 30 BP (Poz-61583), 3520–3355 cal BC), thereby providing a suitable sample for dietary studies using stable isotope analysis.

The Kretuonas 1B cemetery located in northeastern Lithuania revealed interesting dating results. AMS ¹⁴C dates from graves 1 and 3 have been previously reported (5350 ± 130 BP (OxA-5935), 4460–3820 cal BC and 5580 ± 65 BP (OxA-5926), 4550–4330 cal BC, respectively) (Antanaitis-Jacobs et al., 2009). In 2014 we attempted to date bones from graves 1, 3, 4 and 5, and they all yielded similar results - insufficient bone collagen preservation. The last attempt to extract and date collagen from a human canine tooth from grave 5 yielded sufficient collagen and was dated to the Subneolithic period (5540 ± 35 BP (Poz-64677), 4450–4340 cal BC). This date is very similar in age to the AMS dates that were made by the Oxford Radiocarbon Accelerator Unit. The new date also confirms the narrow chronology of the Kretuonas 1B cemetery. It was most likely only used for several tens to several hundred years during the period of 4500–4300 cal BC, and its short usage appears to be the exception rather than the rule for Stone Age cemeteries in the Eastern Baltic. For instance, the Zvejnieki cemetery in Latvia, as well as the Spiginas and Donkalnis cemeteries in Lithuania were in use for several thousands of years during the Mesolithic, Subneolithic, and Neolithic (Zagorskis, 2004; Butrimas, 1992; Butrimas et al., 1985).

AMS 14 C dating was conducted on two Neolithic CWC single graves from Gyvakarai and Biržai. The grave from Gyvakarai has been 14 C dated twice (3745 ± 70 BP (Ki-9470), 2440–1950 cal BC and 3710 ± 80 BP (Ki-9471), 2400–1890 cal BC) (Tebelškis and Jankauskas, 2006). These dates appear to be too young, as the associated burial artefacts (flint and stone axes, and a bone pin) should be attributed typologically to the classical CWC period, i.e. 2800–2400 cal BC. Doubts regarding the earlier dates were supported by a single new AMS 14 C date (4030 ± 30 BP (Poz-61584), 2620–2470 cal BC) which produced a significantly older age that fits completely with our expectations based on artefact typology. Another CWC grave, discovered recently and partially destroyed during construction works at Biržai city (Duderis, 2015), revealed almost the same age as the burial from Gyvakarai (3955 ± 30 BP (Poz-64678), 2570–2350 cal BC).

The last AMS 14 C dates were obtained for the Turlojiškė sacrificial site; where disarticulated human remains with signs of fatal blunt force cranial injuries were discovered within sediments of a boggy lake (Merkevičius, 2012). Three Turlojiškė humans were dated directly by 14 C, although two AMS dates (2895 ± 55 BP (OxA-5931), 1230–920 cal BC and 2835 ± 55 BP (OxA-5927),

1190–840 cal BC) differ significantly from the single date obtained by the beta decay radiocarbon method for grave 3 (3570 \pm 130 BP (Vs-1097), 2300–1560 cal BC) (Antanaitis-Jacobs et al., 2009). We hypothesise that rather than a prolonged continuation of the deposition of human sacrifices at Turlojiškė, the ¹⁴C date analysed at the Vilnius lab might be an outlier. An AMS date for grave 3 revealed a Late Bronze Age date (2730 \pm 30 BP (Poz-66904), 930–810 cal BC), rather than Neolithic or EBA.

The aquatic radiocarbon reservoir effects on the dating of human bones and correction factors have been already estimated and discussed elsewhere for the coastal Subneolithic Šventoji sites (Piličiauskas et al., 2017b). For Mesolithic-Subneolithic skeletons from the Spiginas and Donkalnis cemeteries, both located on Lake Biržulis, the fresh water reservoir effect (FRE) may have been only minimal, as has been shown by paired dates of humans and ungulates (Piličiauskas and Heron, 2015). δ^{13} C and δ^{15} N stable isotope values indicate that the dates of the samples from the Neolithic CWC, as well as of EBA humans, are also not affected by the FRE because the of the marginal role of freshwater food in the diet (see following section). The only dates that may be significantly affected by FRE are from the Kretuonas 1B cemetery. Even here, assuming a significant FRE, for example 1000 years (see Piličiauskas and Heron, 2015), the site chronology would not exceed the upper boundary of the Subneolithic, i.e. it would only change from 4400–4300 to 3200–3100 cal BC.

The AMS ¹⁴C re-dating of previous ¹⁴C dated human remains revealed important information. Significantly different ages were obtained in all three cases (Spiginas, Gyvakarai, Turlojišlė). In a single case an AMS 14 C date appeared to be older by 300 ± 61 radiocarbon years (Gyvakarai CWC single grave), while in two cases (Spiginas and Turlojiškė) the AMS dates were younger than the beta decay method dates by 500 ± 134 and 840 ± 133 radiocarbon years, respectively. To these, we can also add already published paired dates for the CWC grave 3 from Benaičiai with an age difference of 1350 ± 76 radiocarbon years, although in this case, a goat and human bone were dated instead of sampling the same individual (Piličiauskas et al., 2017b). In addition, only one of five known cases of paired beta decay and AMS dates for human remains (Spiginas, burial 1) shows overlap in the 2 sigma ranges (4320–3370 and 4440–4240 cal BC) although the AMS date greatly refines the chronology because of the extremely large uncertainty that was produced by the Geological Institute laboratory in Russia (Fig. 2; Piličiauskas and Heron, 2015). Differences between the previous dates obtained at various conventional laboratories and recent AMS dates of the same contexts or individuals are evident enough to conclude that previous dates of bone collagen should be treated with caution in all cases. We do not discuss here the possible factors causing errors with the dates made on bone collagen, although some of them, i.e. the condition of the bone and the chemical pre-treatment protocol, have been mentioned elsewhere (e.g. Piličiauskas and Heron, 2015).

Stable isotope measurements of bone collagen data for humans and animals

All human stable isotope results, including previously published data, are reported in Table 3. We also report samples that did not produce sufficient collagen for stable isotope analysis, four from NAU and two from UoY. Only two of the human samples, both from the Subneolithic Kretuonas 1B cemetery, fall outside the acceptable range of C:N ratios of 2.9–3.6 (DeNiro, 1985), and these samples are not included in the discussion.

All 17 animal bone samples were analysed at NAU, with 14 samples originating from the inland Žemaitiškė 2 site (Table 1). All animal sample values fell in the acceptable range for C:N ratios and collagen quality (DeNiro, 1985; van Klinken, 1999). In total, with previously published data, 83 stable isotope values are available for Lithuanian Subneolithic-Bronze Age fauna (Table 4).

Inter-laboratory comparison of carbon and nitrogen stable isotope data

During repeated analysis of human bone collagen carbon and nitrogen stable isotopes, we found significant pairwise differences of up to 0.9 % $_{0}$ for δ^{13} C and 1.5 % $_{0}$ for δ^{15} N between values previously reported from analysis undertaken at the MPI (Antanaitis-Jacobs et al., 2009) and the NAU labs on the same skeletons (Tables 3 and 5). It was not clear, however, which skeletal element was sampled by the MPI. In order to understand such differences, we ran new measurements at the UoY. The analyses conducted at the UoY lab were run on the same bones as the analyses conducted by NAU. We hypothesised that if the main cause of the inter-laboratory differences was due to the analysis of different skeletal elements, then the measurements from UoY should demonstrate a better agreement with the values from NAU. This, however, was not the case. We found pairwise differences of up to 1.1 % 13 C and 1.9 % 15 N between values of the NAU and the UoY (Table 5).

A plot of δ^{13} C and δ^{15} N values of the same individuals measured at three different labs clearly demonstrates that analysis of the same bone (NAU and UoY) do not guarantee the same stable isotope data (Fig. 3). However, in just one case (i.e. δ^{15} N UoY-NAU) do our observed average inter-laboratory pairwise differences exceed the values (0.2 ‰ for δ^{13} C and 0.4 ‰ for δ^{15} N) reported by Pestle et al.'s (2014) inter-laboratory study. It is possible that the isotopic variability among the NAU-MPI and the UoY-MPI laboratories may be attributed to differences in sample preparation and analysis, although the MPI protocol was very similar to that used at UoY. Although such processes are currently unknown, pathological conditions can also introduce significant intraelement isotopic variation to magnitude of 0.6 ‰ for δ^{13} C and 2.5 ‰ for δ^{15} N (Olsen et al., 2014) and could be significant here. It is important to note that these observed differences do not change our overall interpretation and reconstruction of diet (Fig. 3). Comparison and modelling of individual diets is not a sensible approach in dietary studies when differences in δ^{13} C and δ^{15} N are less than 1 ‰.

Dietary differences between the last hunter-gatherers and the first farmers

All available wild animal stable isotope data (Table 4; Fig. 4) is used to construct a single dietary baseline as the values do not demonstrate any significant discrepancies in regard to specific region or time period. For example, auroch/bison from north-eastern Lithuanian Subneolithic-EBA sites have average $\delta^{13}C$ and $\delta^{15}N$ values of -22.6 ‰ and 4.5 ‰ (n=3), while the same species from the coastal Šventoji sites have average values of -22.5 ‰ and 4.3 ‰ (n=2). Coastal elk do not differ from their inland counterparts (-23.4 ‰ and 4.3 ‰ (n=3); -23 ± 0.1 ‰ and 4.1 ‰ (n=2)). Contrary to what might be expected, omnivorous bears from coastal sites do not demonstrate a significant marine diet. Their $\delta^{13}C$ values are only slightly more negative compared to inland animals (-21.2 ± 0.3 ‰; n=3 and -20.6 ± 0.4 ‰; n=3 respectively) and their $\delta^{15}N$ values do not differ substantially (4.9 ± 0.7 ‰ and 4.8 ± 0.2 ‰). As distinct from bears, coastal boars have slightly less negative $\delta^{13}C$ values compared to inland animals (-21.7 ± 0.1 ‰ (n=2) and -22.9 ± 0.5 ‰ (n=3) respectively), although $\delta^{15}N$ values are not significantly different, perhaps because the $\delta^{15}N$ values of inland boars are highly varied (5.1 ± 1.3 ‰).

Distinct from the mammal data discussed previously, the stable isotope values of lagoonal freshwater fish ($\delta^{13}C = -21.6 \pm 1 \%$; $\delta^{15}N = 11.2 \pm 1.4 \%$; n=5) differ significantly from those of the same species living in inland rivers or lakes. For Lithuania, all data comes from the Šventoji Subneolithic sites dated to ca. 3000 cal BC and situated at a former lagoon. Pike, perch and pikeperch bones were investigated (Table 4; Piličiauskas et al. 2017b). Although there are no data from Lithuanian inland freshwater species, data from Latvia demonstrate that Subneolithic freshwater fish from the Burtnieki Lake had much more negative $\delta^{13}C$ values ($\delta^{13}C = -27.8 \pm 1.4 \%$; $\delta^{15}N = 9.2 \pm 1.4 \%$; n=35) (Schmölcke et al., 2015). The very specific diet of coastal Subneolithic dogs as well as the stable isotope values of seals are discussed elsewhere (Piličiauskas et al., 2017b).

Overall, Lithuanian Stone and Bronze Age human stable isotope data cluster into four distinct dietary groups (Fig. 4), related to different subsistence economies determined by both local ecology and cultural changes through time. We note, however, that there lacks chronological representativeness as there are no data from the Final Palaeolithic, Early Mesolithic, Early Bronze Age, as well as from any period of the coastal zone with the exception of very late Subneolithic and Neolithic (3200–2400 cal BC). The total number of human samples is small due to poor collagen preservation in a significant proportion of those sampled. For this study our success rate was 69.4%, i.e. collagen was preserved and gave reliable results for 25 humans of the 36 individuals sampled.

Mann-Whitney U tests were performed to compare the inland Late Mesolithic ($\delta^{13}C = -22.6 \pm 0.3\%$; $\delta^{15}N = 12.3 \pm 1\%$; n=6) and inland Subneolithic ($\delta^{13}C = -22.5 \pm 0.5\%$; $\delta^{15}N = 12 \pm 0.7\%$; n=7) $\delta^{13}C$ and $\delta^{15}N$ values. Mean $\delta^{13}C$ values were -22.6%, and the 7 Subneolithic $\delta^{13}C$ values have higher mean ranks (7.43) than the 6 Late Mesolithic values (6.50), (U=18, p=0.668). Mean $\delta^{15}N$ values were 12.2%, and the 6 Late Mesolithic $\delta^{15}N$ values have higher mean ranks (7.17) than the 7 Subneolithic values (6.86), (U = 20, p = 0.886). Analyses show no statistical differences in diet between these populations, therefore these are discussed together (Fig. 4). As the

Subneolithic is a cultural horizon marking the introduction of pottery, it is interesting to note that this technology did not significantly change the protein sources eaten by hunters-gatherers, despite the new opportunities for food preparation and storage. When compared to other isotope data from the Eastern Baltic (Fig. 5), the inland Mesolithic-Subneolithic people of Lithuania (δ^{13} C = -22.7 ± 0.5 %; δ^{15} N $12 \pm 0.9 \%$; n=15) had similar diets to the contemporaneous population at Zvejnieki in northern Latvia (δ^{13} C = -22.8 ± 1.3 % $_{o}$; δ^{15} N 12.4 ± 1.2 % $_{o}$; n=34; Eriksson et al., 2003). Our data suggest that, overall, inland south-eastern Baltic hunter-gatherers had mixed diets of freshwater fish and hunted forest animals, perhaps with a greater contribution of the former. This is supported by both the zooarchaeological evidence (e.g. Schmölcke et al., 2015) and stable isotope data (Fig. 4) but contrasts with evidence of a dominance of aquatic products in Subneolithic pottery, supporting the notion that the latter was used highly selectively (Heron et al. 2015; Oras et al. 2017). Similar stable isotopic dietary evidence has been reported in contemporaneous populations in Estonia and north-western Russia (Tõrv and Meadows, 2015; Wood et al., 2013). These estimations, however, do not consider the contribution of low protein wild plant foods to diet, which was likely to have been significant. For example, based on the isotope analysis undertaken at Zvejnieki, it is estimated using a Bayesian model that plant foods provided 25-50% of the calorific intake during the Subneolithic Narva phase (Meadows et al., 2016).

In contrast, the coastal Subneolithic groups relied strongly on lagoon fishing, while seals and forest game were of much lesser importance (Piličiauskas et al., 2017b). The coastal Subneolithic people are clearly distinguished isotopically from inland Subneolithic people (Fig. 4). This can be explained by the consumption of lagoonal freshwater fish, which were enriched in 13 C and 15 N compared to inland freshwater resources. The Lithuanian Subneolithic coastal peoples (δ^{13} C $-19.9 \pm 0.8 \% c; \delta^{15}$ N 14.8 $\pm 0.6 \% c;$ n=5; Piličiauskas et al., 2017b) were not dedicated seal hunters such as those documented from the contemporaneous PWC communities on Gotland, Sweden (δ^{13} C $-15 \pm 0.6 \% c;$ δ^{15} N 15.9 $\pm 0.6 \% c;$ n=37; Eriksson, 2004) even though they would have had access to the same marine ecosystem. Their isotope values are instead more similar to the Neolithic individuals buried in the Ostorf cemetery in northern Germany, who relied heavily on freshwater fish (δ^{13} C $-20.4 \pm 0.8 \% c;$ δ^{15} N 13.8 $\pm 0.9 \% c;$ n=15; Lübke et al., 2009). This similarity, however, is most likely not caused by similar diets at the German and Lithuanian sites, since Ostorf is located a significant distance from the coast, while the Šventoji sites were situated on the coast of the former lagoon, i.e. near the sea. The differences in geographical location most likely reflect differences in isotopic baselines.

A major dietary shift is seen with the introduction of Neolithic Corded Ware culture at around 2900–2400 cal BC. The Neolithic Corded Ware people in Lithuania ($\delta^{13}C = -21.5 \pm 0.4 \%$; $\delta^{15}N = 10.1 \pm 0.8 \%$; $n=10^{-2}$), Latvia ($\delta^{13}C = -21.7 \pm 0.3 \%$; $\delta^{15}N = 10.1 \pm 0.3 \%$; $n=4^{-3}$; Eriksson et al., 2003), north-eastern Poland (Niedrzwica site; $\delta^{13}C = -21.6 \%$; $\delta^{15}N = 10.2 \%$; Reitsema et al., 2010), and central Poland (Kruszyno site; $\delta^{13}C = -21.9 \%$; $\delta^{15}N = 10.2 \%$; Pospieszny et al.,

² The Benaičiai infant's values are excluded. Number of measurements are given. Number of individuls is lower (n=6).

³ The Selgas 2 infant's values are excluded.

2015) share a similar protein diet (Fig 5), and all differ from Late Mesolithic-Subneolithic huntergatherers. The data are consistent with animal products, most likely meat and milk of sheep or goats, given the faunal assemblages (Piličiauskas et al. 2016b; Lõugas et al., 2007), providing the main source of protein during the Neolithic CWC. It may also be noted that the Globular Amphora Culture (GAC) people in South-Eastern Poland have similar isotopic values ($\delta^{13}C = -20.7 \pm 0.4 \% e$; $\delta^{15}N = 10.6 \pm 0.5 \% e$; n=15; Eriksson and Howcroft, 2014) to the South-Eastern Baltic CWC. More substantial zooarchaeological collections from the GAC settlements indicate a greater dietary role of cattle and pigs for the GAC people compared to the CWC people (Szmyt, 1996).

A certain contribution of freshwater food in the diet of the South-Eastern Baltic CWC is also evident. An individual from Biržai highlights this point. In addition to the collagen stable isotope data from bone, we also determined the stable isotope values of dentine collagen from the teeth from one adult male (Fig. 4). This approach is frequently used to understand variability in diet during life, as unlike bone, tooth dentine does not turnover, meaning it can provide information on childhood diet whilst the teeth were forming (Hillson, 2005; Eriksson and Lidén, 2013). An adult male from a Biržai single grave died at the age of 30 to 35 and was then buried according customs of the Corded Ware Culture, in a crouched position and with a large boar tusk, flint axe, and knife. Interestingly, there is a discrepancy in the δ^{13} C and δ^{15} N values between the different tissues analysed. Dentine from the 3rd molar of this individual is over 2% enriched in ¹⁵N compared to the 1st and 2nd molars, indicating a shift to a diet richer in freshwater fish when this tooth was forming during the individual's teenage years. The bone collagen value represents diet over at least the last several decades before death and particularly during adolescence (Hedges et al., 2007), and is intermediate between these values, perhaps reflecting a shift to more terrestrial foods later in this individual's life. Importantly, evidence of freshwater fish is only visible isotopically by sampling tissues that form over short periods. The longer averaged dietary record provide by bone shows a more mixed signal dominated by terrestrial protein (Fig 4). Such sporadic consumption of fish has been noted before in coastal Neolithic populations (Montgomery et al. 2013), and shows the highly flexible subsistence strategy of the CWC people living in this region.

Another argument that freshwater food may have made up a considerable part of the CWC people's diet during particular periods is the slightly more negative $\delta^{13}C$ and slightly more elevated $\delta^{15}N$ values of some individuals (e.g. Gyvakarai grave; $\delta^{13}C$ -21.9 %; $\delta^{15}N$ 10.1 %) compared to the typical Neolithic and Bronze Age farming populations of the Baltic region (Fig. 5). It should also be noted that Swedish CWC people were not dedicated farmers or herders, as their stable isotope data shows that marine foodstuffs were consumed in significant quantities in coastal areas (Fig. 5; Fornander, 2013).

There is a lack of human remains from the period of 2000–1300 cal BC or the EBA. Grave 2 from the Spiginas cemetery (2130–1750 cal BC) is the only individual that can be attributed to the transition between Neolithic and EBA. The closest stable isotope data to that of the EBA comes from Estonia. Human remains from the Kivisaare I and Riigiküla cemeteries show stable isotope values (δ^{13} C -21.8 ± 0.4 % $_c$; δ^{15} N 11.2 ± 0.6 % $_c$; n=4; Tõrv and Meadows, 2015) that are similar to those of Lithuanian CWC people.

The Late Bronze Age diet (δ^{13} C -17.8 ± 0.6 %; δ^{15} N 9.5 ± 0.4 %; n=5) is very distinct compared to all other groups (Fig. 4). The 5 individuals from Turlojiškė have collagen enriched in 13 C but relatively depleted in 15 N indicating much greater reliance on plant foods, including millet, at around 1000 cal BC, consistent with the large scale adoption of agriculture. Millet is a C₄ plant with carbon isotope values that are significantly enriched in 13 C compared to C₃ plants, such as barley or wheat (DeNiro, 1987). Burnt millet (*Panicum miliaceum*) grains are found at Turlojiškė and dated to 2590 ± 75 BP (Ua-16681), 910–485 cal BC (Antanaitis and Ogrinc, 2000). A subsistence economy including millet is also found later, in Roman or even Medieval Poland (Reitsema et al. 2010), although it is absent in Estonia and Latvia during the Late Bronze Age (Fig. 5; Laneman, 2012; Laneman and Lang, 2013). This suggests that the northern boundary between millet-cultivating and non-millet cultivating peoples ran somewhere through northern Lithuania or southern Latvia around 1000 cal BC and may define environmental limits for production of this crop.

Although stable isotope data cannot specifically answer the question as to the importance of domesticated crops to the economy of the first farmers, the macrobotanical data indicates that intensification and consolidation of this new subsistence economy was a slow and gradual process which only became fully established in the middle of the Bronze Age (Piličiauskas et al., 2017a). The oldest evidence for crop cultivation in the East Baltic comes from the western Lithuanian Kvietiniai multi-period site where a charred barley grain was dated to ca. 1400/1200 cal BC (Vengalis et al., in prep).

Conclusions

New AMS dates obtained from Mesolithic-Late Bronze Age Lithuanian graves and isolated human bones have helped to refine the chronology of this period. In four out of five cases, the repeated AMS dating of human remains revealed large discrepancies between previous ¹⁴C dates and recent AMS dates in the order of magnitude from several hundred to one-thousand radiocarbon years. Such results highlight the need for re-dating (including rigorous procedures of collagen preservation assessment, pre-treatment and ultrafiltration) of all prehistoric human remains where chronology was previously based on ¹⁴C dating of bone collagen made at conventional dating labs.

Four distinct diets may be interpreted from the analysis of stable isotopes in human and faunal samples. These diets relate to different subsistence economies determined by both local ecology and cultural changes:

- Inland Mesolithic-Subneolithic hunters-gatherers (7000–3000 cal BC) consumed a mixed diet of freshwater food and hunted forest animals, although a substantial amount of foraged plant foods is also likely.
- The coastal Subneolithic (3000 cal BC) groups relied heavily on lagoon fishing, while seals and forest game were of much lesser importance.
- Animal husbandry, most likely of sheep or goats, was a main source of protein for the Neolithic Corded Ware Culture (2900–2400 cal BC) people, although freshwater fish were

- also consumed. The Biržai Neolithic adult male demonstrated significant intra-individual variation of δ^{15} N, highlighting the highly flexible subsistence strategy of the CWC people.
- Unusually high δ^{13} C values indicate that millet was introduced into the farming economy of the Late Bronze Age people around 1000 cal BC or even earlier however. Unfortunately, a large gap with no stable isotope data exists between 2000–1300 cal BC due to the extreme rarity of Early Bronze Age human remains.

The human and animal stable isotope data presented here supports the premise that agriculture in the eastern Baltic started 1000 years later than in the southwestern Baltic. The most likely driver for this economic transition was the arrival of migrants from the Pontic steppe synonymous with the Corded Ware cultural phenomenon (Haak et al., 2015). At this time the people of the Corded Ware Culture may have introduced new animals and possibly domesticated plants. Archaeological evidence demonstrates that the last hunter-fishers in particular regions lived side-by-side with the farmers for a rather long period in the east Baltic, and such a situation represents an intriguing opportunity to learn about various cultural, socioeconomic and possible even genetic encounters, and palaeodiet may be one of possible expressions of those processes.

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Tables

No	Site	Site function	Time newied	AMS	S 14C	δ ¹³ C aı	$10 \delta^{15}N$
110	Site	Site function	Time period	Humans	Animals	Humans	Animals
1	Biržai	single grave	Neolithic	1(1)		1 (1)	
2	Daktariškė 1	dwelling area	Subneolithic-Neolithic	1(1)		1 (1)	
3	Daktariškė 5	refuse zone	Subneolithic-Early Bronze Age				1(1)
4	Donkalnis	cemetery	Late Mesolithic-Neolithic	3 (3)		6 (6)	
5	Gyvakarai	single grave	Neolithic	1(1)		1 (1)	
6	Kretuonas 1B	cemetery	Subneolithic	6 (1)		6 (1)	
7	Nida	dwelling area	Subneolithic-Neolithic				2 (2)
8	Plinkaigalis	single graves	Neolithic			2 (2)	
9	Spiginas	cemetery	Late Mesolithic-Neolithic	1(1)	1 (0)	4 (4)	
10	Turlojiškė	sacrificial site	Late Bronze Age	1(1)		4 (4)	
11	Žemaitiškė 2	refuse zone	Subneolithic-Early Bronze Age				14 (14)
Total	1	<u> </u>	<u> </u>	14 (9)	1 (0)	25 (20)	17 (17)

Table 1. Sites investigated and the number of humans and animals analysed in this study. Total number analysed are shown without brackets and the number for which satisfactory results were obtained are shown in brackets.

No	site, cemetery	¹⁴ C date, years BP	cal BC (95.4%)	% collagen	%C	%N	description	period, culture	reference
1	Benaičiai	4025 ± 30 (Poz-66923)	2620–2470				grave 1, female, >40, skull	Neolithic, CWC	Piličiauskas et al., 2017b
2	Benaičiai	2690 ± 70* (Ki-10632)	1020–670*				grave 3, goat bone	Neolithic, CWC	Merkevičius, 2005
3	Benaičiai	4040 ± 30 (Poz-61591)	2830–2470				grave 3, infant, 0–1	Neolithic, CWC	Piličiauskas et al., 2017b
4	Biržai	3955 ± 30 (Poz-64678)	2570–2350	7.2	11.4	4	grave, male, 30–35, phalanx	Neolithic, CWC	this study
5	Daktariškė 1	4635 ± 30 (Poz-61583)	3520–3355	6.7	6.6	1.4	loose bone, human skull	Subneolithic	this study
6	Donkalnis	7405 ± 45 (CAMS- 85221)	6400–6110				grave 2, male, 20–25	Mesolithic	Antanaitis-Jacobs et al., 2009
7	Donkalnis	5785 ± 40 (CAMS- 85220)	4730–4530				grave 3, female, 25–30	Subneolithic	Antanaitis-Jacobs et al., 2009

8	Donkalnis	6995 ± 65 (OxA-5924)	6000–5740				grave 4, male, 50–55	Mesolithic	Antanaitis-Jacobs et al., 2009
9	Donkalnis	6960 ± 40 (Poz-61575)	5970–5740				grave 4, elk (?) incisor	Mesolithic	Piličiauskas and Heron, 2015
10	Donkalnis	7140 ± 40 (Poz-61589)	6075–5920	2.3	5.9	1.4	grave 5, child, ~7, femur	Mesolithic	this study
11	Donkalnis	7110 ± 40 (Poz-61588)	6060–5900	10	10.8	3.7	grave 5, newborn, femur	Mesolithic	this study
12	Donkalnis	5770 ± 40 (Poz-61574)	4720–4530	7.3	10.9	3.9	grave 6, female, 35–40, fibula	Subneolithic	this study
13	Donkalnis	6220 ± 90 (Poz-61576)	5460–4940	2.3	5.9	1.4	grave 7, male, >45. Elk/red deer incisor	Mesolithic	Piličiauskas and Heron, 2015
14	Gyvakarai	3745 ± 70* (Ki-9470)	2440–1950*				grave, male, 35–45	Neolithic, CWC	Tebelškis and Jankauskas, 2006
15	Gyvakarai	3710 ± 80* (Ki-9471)	2400–1890*				grave, male, 35–45	Neolithic, CWC	Tebelškis and Jankauskas, 2006
16	Gyvakarai	4030 ± 30 (Poz-61584)	2620–2470	4.5	5.4	1.6	grave, male, 35–45, fibula	Neolithic, CWC	this study
	Kretuonas 1B	not enough	collagen				grave 2, juvenile, 14–16, radius		this study
17	Kretuonas 1B	5350 ± 130 (OxA-5935)	4460–3820				grave 1, female, 20–25	Subneolithic	Antanaitis-Jacobs et al., 2009
	Kretuonas 1B	not enough	collagen				grave 1, female, 20–25, humerus		this study
18	Kretuonas 1B	5580 ± 65 (OxA-5926)	4550–4330				grave 3, male, 50–55	Subneolithic	Antanaitis-Jacobs et al., 2009
	Kretuonas 1B	not enough	collagen				grave 3, male, 50–55, radius		this study
	Kretuonas 1B	not enough	, ,				grave 4, female, >55, radius		this study
	Kretuonas 1B	not enough	, and the same of				grave 5, male, 25–30, radius		this study
19	Kretuonas 1B	5540 ± 35 (Poz-64677)	4450–4340	2.8	10	3.8	grave 5, male, 25–30, canine tooth	Subneolithic	this study
	Kretuonas 1B	not enough	collagen				grave 6, child, <3, metatarsal		this study
20	Plinkaigalis	4030 ± 55 (OxA-5928)	2860–2410				grave 241, female, 50–55	Neolithic, CWC	Antanaitis-Jacobs et al., 2009
21	Plinkaigalis	4280 ± 75 (OxA-5936)	3260–2630				grave 242, female, >40	Neolithic, CWC	Antanaitis-Jacobs et al., 2009
22	Spiginas	5020 ± 200* (Gin-5569)	4320–3370*				grave 1, male, 35–45	Subneolithic	Butrimas et al., 1985
23	Spiginas	5470 ± 40 (Poz-61572)	4440–4240				grave 1, male, 35–45, femur	Subneolithic	Piličiauskas and Heron, 2015
24	Spiginas	5370 ± 40 (Poz-61569)	4330–4060				grave 1, ungulate long bone	Subneolithic	Piličiauskas and Heron, 2015
25	Spiginas	7470 ± 60 (Gin-5571)	6440–6230				grave 4, female, 30–35	Mesolithic	Butrimas et al., 1985
26	Spiginas	4080 ± 120* (Gin-5570)	2910–2300*				grave 2, male, 50–55	Neolithic/EBA	Butrimas et al., 1985

27	Spiginas	3580 ± 60 (Poz-61573)	2130–1750	0.9	5.2	1.3	grave 2, male, 50–55, ulna	Neolithic/EBA	this study
28	Spiginas	7780 ± 65 (OxA-5925)	6800–6460				grave 3, female, ?	Mesolithic	Antanaitis-Jacobs et al., 2009
29	Spiginas	175 ± 30 (Poz- 61571)	1660 AD	11	10.7	3.7	grave 3, ungulate long bone	Modern	this study
30	Šventoji 4	4330 ± 80 (Poz-61577)	3335–2700				loose bone, male, >50, skull	Subneolithic/N eolithic	Piličiauskas et al., 2017b
31	Šventoji 6	290 ± 30 (Poz- 61578)	1490–1660 AD				loose bone, metacarpal	Modern	Piličiauskas et al., 2017b
32	Šventoji 6	4655 ± 35 (Poz-71524)	3620–3360				loose bone, maxilla	Subneolithic	Piličiauskas et al., 2017b
33	Šventoji 23	4580 ± 30 (Poz-61579)	3500–3120				loose bone 1, male, 25–35, mandible	Subneolithic	Piličiauskas et al., 2017b
34	Šventoji 23	4740 ± 35 (Poz-61581)	3640–3380				loose bone 2, adult, maxilla	Subneolithic	Piličiauskas et al., 2017b
35	Šventoji 23	4730 ± 35 (Poz-61582)	3635–3380				loose bone 3, child, 7–11, mandible	Subneolithic	Piličiauskas et al., 2017b
	Šventoji 26	not enough	collagen				loose bone, femur		Piličiauskas et al., 2017b
36	Turlojiškė	2895 ± 55 (OxA-5931)	1230–920				grave 'Kirsna', male, 25–30	LBA	Antanaitis-Jacobs et al., 2009
37	Turlojiškė	2835 ± 55 (OxA-5927)	1190–840				grave 1, male, 25–30	LBA	Antanaitis-Jacobs et al., 2009
38	Turlojiškė	3570 ± 130* (Vs-1097)	2300–1560*				grave 3, male, 25–30	LBA	Antanaitis-Jacobs et al., 2009
39	Turlojiškė	2730 ± 30 (Poz-66904)	930–810	13	11.7	4.1	grave 3, male, 25–30, ulna	LBA	this study

Table 2. ¹⁴C dates and unsuccessful dating attempts (not counted, distinguished by italic) of individuals or loose human bones from 7000–500 cal BC in Lithuania. EBA – Early Bronze Age, LBA – Late Bronze Age. * – outliers or unreliable dates. Dates of the same grave are shaded

				MPI				N	A U					U	οY		
No	Site	sample	δ ¹³ C (%o)	δ ¹⁵ N (‰)	C:N	δ ¹³ C (‰)	δ ¹⁵ N (‰)	C:N	% collag en	%C	%N	δ ¹³ C (‰)	δ ¹⁵ N (%o)	C:N	% collag en	%C	%N
1	Benaičiai	grave 1, mandible				-21.2	9.9	3.3	5.1	37.5	13.5						
2	Benaičiai	grave 1, mandible				-21.2	9.8	3.2	5.8	37.4	13.6						
3	Benaičiai	grave 3, skull				-21.4	10.6	3.3	12.9	39.7	14.2						

4	Benaičiai	grave 3, skull				-21.3	10.9	3.2	15.1	44.5	16.1						
5	Biržai	grave, phalanx				-22.0	11.0	3.2	19.8	43.8	16.3						
6	Biržai	grave, M1 U.L. root				-21.4	9.7	3.1	17.6	45.5	17.2						
7	Biržai	grave, M2 U.L. root				-21.1	9.5	3.1	17.9	45.1	17.0						
8	Biržai	grave, M3 L.R. root				-22.1	11.9	3.1	18.1	44.1	16.6						
9	Daktariškė 1	loose bone, skull				-21.9	12.9	3.3	8.3	32.7	11.6						
10	Donkalnis	grave 1, femur	-23.2	10.6	3.2	-23.5	11.7	3.3	7.4	37.1	13.2	-24.3	12	3.2	4.4	44.8	16.1
11	Donkalnis	grave 2	-22.6	12.4	3.3												
12	Donkalnis	grave 3	-22.1	11.7	3.3												
13	Donkalnis	grave 4, ulna	-22.8	12.5	3.6	-22.7	12.4	3.3	5.9	41.8	14.9						
14	Donkalnis	grave 5 (infant), femur				-22.6	14.0	3.3	13.9	40.2	14.4						
15	Donkalnis	grave 5 (child), femur	-22.1	10.6	3.4	-22.2	12.1	3.3	6.1	43.8	15.7						
16	Donkalnis	grave 6, fibula	-22.1	10.3	3.2	-22.5	11.5	3.3				-22.4	11.6	3.2	10.9	45.1	16.4
17	Donkalnis	grave 7, fibula	-22.4	9.6	3.3	-22.7	10.6	3.2				-21.6	11.5	3.3	3.1	43.2	15.1
18	Donkalnis	grave, disturbed	-23.2	10.4	3.3												
19	Gyvakarai	grave, fibula	-21.9	10.1	3.3	-22.1	10.4	3.2	8.7	44.4	16.2						
20	Kretuonas 1B	grave 1, radius	-23.4	11.3	3.2	not end	ough col	lagen	0.2								
21	Kretuonas 1B	grave 2, femur				1	no peaks		2.2								
22	Kretuonas 1B	grave 3, humerus	-23.2	11.8	3.2	-22.4	11.8	3.2	3.7	35.4	12.8	-22.8	11.8	3.3	1.2	41.9	14.9
23	Kretuonas 1B	grave 4, fibula				-21.9	10.3	8.6	1.4	10.6	1.4						
24	Kretuonas 1B	grave 5, radius				-23.4	10.9	5.4	0.5	13.0	2.8						
25	Kretuonas 1B	grave 6, radius				no peak	9.7		1.4		0.5						
26	Plinkaigalis	grave 241, femur	-21.4	8	3.3	-21.4	8.9	3.3	10.5	43.4	15.6	-21.6	9.4	3.3	4.2	43.3	15.4
27	Plinkaigalis	grave 242, temporal	-21.6	9.9	3.3	-21.5	9.8	3.3	7.1	31.3	11.1						
28	Spiginas	grave 1, femur	-23.3	11.8	3.6	-22.4	12.8	3.3	2.8	35.5	12.6	-23.2	12.6	3.4	2.4	43.6	15.0
29	Spiginas	grave 2, ulna	-21.4	9.5	3.3	-21.2	10.1	3.3	5.1	30.5	10.8						
30	Spiginas	grave 3, fibula	-22.9	13.1	3.6	-23.3	11.6	3.2	12.0	43.5	15.7	-23.1	12.6	3.4	2.5	44.1	15.2
31	Spiginas	grave 4, humerus	-22.7	12.6	3.5	-22.4	12.8	3.2	10.5	48.9	17.8						
32	Šventoji 4	loose bone, skull				-20.1	15.6	3.2	6.6	42.3	15.3						
33	Šventoji 6	loose bone, maxilla				-19.5	14.1	3.3	9.7	41.0	14.2						
34	Šventoji 23	loose bone 1, mandible				-18.9	15.0	3.3	17.1	44.9	15.7						
35	Šventoji 23	loose bone 1, M1 L,L, root				-19.3	15.1	3.3	15.3	44.8	16.1						
36	Šventoji 23	loose bone 1, M3 L,R, root				-18.1	15.6	3.2	13.9	44.5	16.4						

37	Šventoji 23	loose bone 2, maxilla				-20.3	14.4	3.4	17.5	41.8	14.4						
38	Šventoji 23	loose bone 2, M1 U,L, root				-19.6	16.0	3.3	9.5	41.8	14.7						
39	Šventoji 23	loose bone 3, mandible				-21.0	15.0	3.3	12.3	33.7	11.8						
40	Šventoji 23	loose bone 3, M1 L,L, root				-21.2	15.3	3.2	10.3	42.9	15.5						
41	Šventoji 26	loose bone, femur				not en	ough col	lagen	0.2			not eno	ugh colla	gen			
42	Šventoji 43	loose bone, M tooth										not eno	ugh colla	gen			
42	Šventoji 43 Turlojiškė	loose bone, M tooth grave 'Kirsna', skull	-18.1	10.1	3.2							not eno	ugh colla	gen			
			-18.1 -18.7	10.1	3.2	-18.0	9.2	3.2	16.7	34.1	12.4	not enor	ugh colla 9.3	gen 3.2	11.4	44.1	15.9
43	Turlojiškė	grave 'Kirsna', skull				-18.0 -16.9	9.2	3.2	16.7 13.9	34.1	12.4 15.4				11.4	44.1	15.9
43	Turlojiškė Turlojiškė	grave 'Kirsna', skull grave 3, ulna	-18.7	9.2	3.3										11.4	44.1	15.9

Table 3. δ^{13} C and δ^{15} N bone collagen values for Lithuanian humans dated to 7000–500 cal BC, including unreliable results and unsuccessful attempts. Measurements made at the MPI have been taken from Antanaitis-Jacobs et al. (2009), while those by NAU and UoY are from this study, with the exception of Benaičiai and Šventoji (Piličiauskas et al., 2017). The same bones were sampled by NAU and UoY and their descriptions are given in the table, whilst skeletal parts sampled at MPI as well as %C and %N values were not reported (Antanaitis-Jacobs et al. 2009). Repeated samples from the same individuals are shaded. For the UoY samples, % collagen yields were calculated from retentate samples only, following ultrafiltration.

No	species	site	period	δ13C (‰)	δ15N (%o)	C:N	% collagen	%C	%N	reference
1	auroch/bison (Bos primigenius B./Bison bonasus bonasus L.)	Kretuonas 1D	Early Bronze Age	-22.3	3.1	3.3				Antanaitis-Jacobs et al. 2009
2	auroch/bison (Bos primigenius B./Bison bonasus bonasus L.)	Šventoji 2/4	Subneolithic	-22.6	5.1	3.1	19.2	39.8	15.0	Piličiauskas et al., 2017b
3	auroch/bison (Bos primigenius B./Bison bonasus bonasus L.)	Šventoji 43	Subneolithic	-22.4	3.4	3.3	2.9	24.0	8.6	Piličiauskas et al., 2017b
4	auroch/bison (Bos primigenius B./Bison bonasus bonasus L.)	Žemaitiškė 2	Subneolithic	-22.6	5.1	3.3	14.1	42.0	15.1	this study
5	auroch/bison (Bos primigenius B./Bison bonasus bonasus L.)	Žemaitiškė 2	Subneolithic	-22.9	5.4	3.3	7.6	40.3	14.4	this study
6	European badger (Meles meles L.)	Žemaitiškė 2	Subneolithic	-19.5	10.1	3.6				Antanaitis-Jacobs et al. 2009
7	brown bear (Ursus arctos L.)	Šventoji 3	Subneolithic	-21.4	4.5	3.3		·		Antanaitis-Jacobs et al. 2009
8	brown bear (Ursus arctos L.)	Šventoji 43	Subneolithic	-21.4	5.7	3.3	3.5	28.1	10.1	Piličiauskas et al., 2017b

9	brown bear (Ursus arctos L.)	Šventoji 6	Subneolithic	-20.9	4.4	3.5				Antanaitis-Jacobs et al. 2009
10	brown bear (Ursus arctos L.)	Žemaitiškė 2	Subneolithic	-20.9	4.6	3.2	10.9	38.7	14.1	this study
11	brown bear (Ursus arctos L.)	Žemaitiškė 2	Subneolithic	-20.1	4.7	3.2	9.8	40.2	14.7	this study
12	brown bear (Ursus arctos L.)	Žemaitiškė 3B	Subneolithic	-20.7	5.0	3.3				Antanaitis-Jacobs et al. 2009
13	beaver (Castor fiber L.)	Šventoji 3	Subneolithic	-22.1	5.4	3.4				Antanaitis-Jacobs et al. 2009
14	beaver (Castor fiber L.)	Šventoji 9	Early Bronze Age	-22.9	4.5	3.2	16.1	41.5	15.3	Piličiauskas et al., 2017b
15	beaver (Castor fiber L.)	Žemaitiškė 2	Subneolithic	-22.6	5.6	3.3	7.3	42.2	15.0	this study
16	beaver (Castor fiber L.)	Žemaitiškė 2	Subneolithic	-23.9	4.8	3.3				Antanaitis-Jacobs et al. 2009
17	beaver (Castor fiber L.)	Žemaitiškė 2	Subneolithic	-22.0	5.5	3.3	9.1	38.6	13.5	this study
18	beaver (Castor fiber L.)	Žemaitiškė 2	Subneolithic	-23.0	3.5	3.5				Antanaitis-Jacobs et al. 2009
19	boar (Sus scrofa scrofa L.)	Šventoji 3	Subneolithic	-21.7	5.5	3.4				Antanaitis-Jacobs et al. 2009
20	boar (Sus scrofa scrofa L.)	Šventoji 6	Subneolithic	-21.6	5.3	3.4				Antanaitis-Jacobs et al. 2009
21	boar (Sus scrofa scrofa L.)	Žemaitiškė 1	Subneolithic	-23.3	6.5	3.5				Antanaitis-Jacobs et al. 2009
22	boar (Sus scrofa scrofa L.)	Žemaitiškė 2	Subneolithic	-23.1	4.6	3.2	3.4	32.8	12.0	this study
23	boar (Sus scrofa scrofa L.)	Žemaitiškė 2	Subneolithic	-22.4	4.1	3.2	14.3	43.7	15.8	this study
24	boar/pig (Sus scrofa scrofa L./Sus scrofa domesticus L.)	Kretuonas 1B	Subneolithic	-23.6	6.4	3.5				Antanaitis-Jacobs et al. 2009
25	boar/pig (Sus scrofa scrofa L./Sus scrofa domesticus L.)	Šventoji 1B	Subneolithic	-21.8	4.1	3.4				Antanaitis-Jacobs et al. 2009
26	boar/pig (Sus scrofa scrofa L./Sus scrofa domesticus L.)	Šventoji 3	Subneolithic	-21.3	3.8	3.3				Antanaitis-Jacobs et al. 2009
27	boar/pig (Sus scrofa scrofa L./Sus scrofa domesticus L.)	Šventoji 43	Subneolithic	-22.2	6.9	3.2	16.1	44.8	16.3	Piličiauskas et al., 2017b
28	boar/pig (Sus scrofa scrofa L./Sus scrofa domesticus L.)	Žemaitiškė 2	Subneolithic	-21.4	3.8	3.3	17.1	44.5	15.8	this study
29	cattle (Bos taurus L.)	Turlojiškė	Late Bronze Age	-21.1	7.4	3.2				Antanaitis-Jacobs et al. 2009
30	cattle (Bos taurus L.)	Žemaitiškė 2	Subneolithic	-22.7	4.8	3.2	13.1	40.5	14.7	this study
31	common goldeneye (Bucephala clangula L.)	Žemaitiškė 2	Subneolithic	-23.3	7.3	3.4				Antanaitis-Jacobs et al. 2009
32	dog (Canis familiaris L.)	Šventoji 23	Subneolithic	-19.2	12.8	3.6				Antanaitis-Jacobs et al. 2009
33	dog (Canis familiaris L.)	Šventoji 43	Subneolithic	-23.8	13.9	3.5	2.2	12.5	4.2	Piličiauskas et al., 2017b
34	dog (Canis familiaris L.)	Šventoji 6	Subneolithic	-20.3	13.2	3.3	11.7	43.0	15.4	Piličiauskas et al., 2017b
35	dog (Canis familiaris L.)	Šventoji 6	Subneolithic	-20.7	13.3	3.4				Antanaitis-Jacobs et al. 2009
36	elk (Alces alces L.)	Šventoji 1B	Subneolithic	-23.1	3.6	3.4				Antanaitis-Jacobs et al. 2009
37	elk (Alces alces L.)	Šventoji 2/4	Subneolithic	-23.6	4.9	3.3				Antanaitis-Jacobs et al. 2009
38	elk (Alces alces L.)	Šventoji 43	Subneolithic	-23.5	4.4	3.3	1.8	37.4	13.1	Piličiauskas et al., 2017b
39	elk (Alces alces L.)	Žemaitiškė 2	Subneolithic	-22.9	4.1	3.3	8.2	44.3	15.9	this study
40	elk (Alces alces L.)	Žemaitiškė 2	Subneolithic	-23.1	4.1	3.3	15.0	45.1	15.9	this study
41	flounder (Platichthys flesus L.)	Šventoji 2/4	Subneolithic	-16.6	11.6	3.3				Antanaitis-Jacobs et al. 2009
43	horse (Equus ferus caballus L.)	Šventoji 41B	Early Bronze Age	-22.3	4.4	3.3	11.3	34.0	12.2	Piličiauskas et al., 2017b
44	horse (Equus ferus caballus L.)	Šventoji 43	Subneolithic	-23.2	4.9	3.2	12.2	39.8	14.6	Piličiauskas et al., 2017b

45	horse (Equus ferus caballus L.)	Šventoji 43	Subneolithic	-24.7	5.7	3.5	1.0	25.7	8.5	Piličiauskas et al., 2017b
46	mallard (Anas platyrhynchos L.)	Šventoji 2/4	Subneolithic	-24.8	7.2	3.3				Antanaitis-Jacobs et al. 2009
47	mallard (Anas platyrhynchos L.)	Šventoji 23	Subneolithic	-21.1	7.8	3.5				Antanaitis-Jacobs et al. 2009
48	mallard (Anas platyrhynchos L.)	Turlojiškė	Late Bronze Age	-19.4	8.4	3.5				Antanaitis-Jacobs et al. 2009
53	northern pike (Esox lucius L.)	Šventoji 2/4	Subneolithic	-22.1	9.5	3.3	2.3	38.5	13.8	Piličiauskas et al., 2017b
54	northern pike (Esox lucius L.)	Šventoji 2/4	Subneolithic	-21.6	12.6	3.3				Antanaitis-Jacobs et al. 2009
49	pine marten (Martes martes L.)	Žemaitiškė 2	Subneolithic	-20.1	8.8	3.5				Antanaitis-Jacobs et al. 2009
50	otter or seal? (<i>Lutra lutra</i> L. or Phocidae?)	Šventoji 23	Subneolithic	-16.5	13.8	3.4				Antanaitis-Jacobs et al. 2009
51	perch (Perca fluviatilis L.)	Šventoji 2/4	Subneolithic	-20.0	10.6	3.3	3.5	36.0	12.7	Piličiauskas et al., 2017b
52	pig (Sus scrofa domesticus L.)	Daktariškė 5	Bronze Age?	-21.7	4.5	3.3	15.2	45.9	16.4	this study
55	pikeperch (Sander lucioperca L.)	Šventoji 2/4	Subneolithic	-22.6	10.9	3.4	1.3	39.9	13.6	Piličiauskas et al., 2017b
56	pikeperch (Sander lucioperca L.)	Šventoji 2/4	Subneolithic	-21.8	12.6	3.5				Antanaitis-Jacobs et al. 2009
57	red deer (Cervus elaphus L.)	Turlojiškė	Late Bronze Age	-22.5	5.5	3.4				Antanaitis-Jacobs et al. 2009
58	red deer (Cervus elaphus L.)	Žemaitiškė 1	Subneolithic	-24.1	4.0	3.5				Antanaitis-Jacobs et al. 2009
59	red deer (Cervus elaphus L.)	Žemaitiškė 2	Subneolithic	-22.3	5.4	3.2	18.8	44.6	16.3	this study
60	red deer (Cervus elaphus L.)	Žemaitiškė 2	Subneolithic	-23.2	4.2	3.2	11.4	38.4	14.0	this study
61	roe deer (Capreolus capreolus L.)	Nida	Neolithic	-21.0	6.1	3.3	11.9	44.3	15.9	this study
62	roe deer (Capreolus capreolus L.)	Šventoji 43	Subneolithic	-23.5	4.5	3.2	12.8	40.9	14.8	Piličiauskas et al., 2017b
42	red fox (Vulpes vulpes L.)	Šventoji 3	Subneolithic	-18.5	11.4	3.4				Antanaitis-Jacobs et al. 2009
63	true seals (Phocidae)	Nida	Neolithic	-15.9	13.4	3.2	2.5	41.8	15.1	this study
64	harbour seal (<i>Phoca vitulina</i> L.)	Šventoji 1B	Subneolithic	-15.5	13.1	3.3				Antanaitis-Jacobs et al. 2009
65	ringed seal (<i>Phoca hispida</i> L.)	Šventoji 1B	Subneolithic	-16.5	11.1	3.4				Antanaitis-Jacobs et al. 2009
66	true seals (Phocidae)	Šventoji 2/4	Subneolithic	-15.3	13.1	3.2				Heron et al. 2015
67	true seals (Phocidae)	Šventoji 2/4	Subneolithic	-16.6	12.0	3.2				Heron et al. 2015
68	ringed seal (<i>Phoca hispida</i> L.)	Šventoji 2/4	Subneolithic	-15.8	12.4	3.3				Antanaitis-Jacobs et al. 2009
69	true seals (Phocidae)	Šventoji 2/4	Subneolithic	-17.7	10.6	3.4				Antanaitis-Jacobs et al. 2009
70	true seals (Phocidae)	Šventoji 2/4	Subneolithic	-16.3	12.2	3.4				Antanaitis-Jacobs et al. 2009
71	harbour seal (<i>Phoca vitulina</i> L.)	Šventoji 2/4	Subneolithic	-16.1	12.0	3.4				Antanaitis-Jacobs et al. 2009
72	ringed seal (<i>Phoca hispida</i> L.)	Šventoji 2/4	Subneolithic	-18.7	13.9	3.4				Antanaitis-Jacobs et al. 2009
73	true seals (Phocidae)	Šventoji 2/4	Subneolithic	-16.3	15.5	3.4				Heron et al. 2015
74	grey seal (Halichoerus grypus L.)	Šventoji 23	Subneolithic	-16.5	12.7	3.5				Antanaitis-Jacobs et al. 2009
75	harp seal (<i>Pagophilus groenlandicus</i> L.)	Šventoji 3	Subneolithic	-15.6	11.3	3.2	23.7	40.7	15.1	Piličiauskas et al., 2017b
76	harp seal (Pagophilus groenlandicus L.)	Šventoji 43	Subneolithic	-16.5	12.7	3.3	3.1	28.2	10.0	Piličiauskas et al., 2017b
77	grey seal (Halichoerus grypus L.)	Šventoji 43	Subneolithic	-16.9	11.7	3.4	2.0	23.7	8.2	Piličiauskas et al., 2017b
78	ringed seal (<i>Phoca hispida</i> L.)	Šventoji 6	Subneolithic	-17.1	12.6	3.4				Antanaitis-Jacobs et al. 2009
79	harp seal (Pagophilus groenlandicus L.)	Šventoji 6	Subneolithic	-16.6	13.3	3.4				Antanaitis-Jacobs et al. 2009
80	grey wolf (Canis lupus L.)	Šventoji 52	Subneolithic	-20.9	9.0	3.2	12.6	41.0	14.8	Piličiauskas et al., 2017b
81	wood grouse (Tetrao urogallus L.)	Šventoji 23	Subneolithic	-21.9	2.2	3.6				Antanaitis-Jacobs et al. 2009

Table 4. $\delta^{13}C$ and $\delta^{15}N$ bone collagen values for Subneolithic-Bronze Age animals in Lithuania

	UoY	Y-MPI	UoY	-NAU	NAU	-MPI	Ave	rage	Sto	lev
Sample	δ ¹³ C	$\delta^{15}N$								
	(%0)	(%o)	(%0)	(%o)	(%0)	(%0)	(%0)	(%0)	(%o)	(%0)
Spiginas, grave 1	-0.8	-0.2	0.1	0.8	-0.9	-1.0	-23.0	12.4	0.5	0.54
Spiginas, grave 3	0.2	1.0	-0.2	-0.5	0.4	1.5	-23.1	12.4	0.2	0.77
Kretuonas 1B, grave 3	-0.4	0.1	0.4	0.0	-0.8	0.1	-22.8	11.8	0.4	0.03
Donkalnis, grave 7	1.1	0.9	0.8	1.9	0.3	-1.0	-22.2	10.6	0.6	0.96
Donkalnis, grave 6	0.1	0.2	-0.3	1.3	0.4	-1.2	-22.3	11.1	0.2	0.72
Donkalnis, grave 1	-0.8	0.3	-1.1	1.4	0.3	-1.1	-23.7	11.4	0.6	0.74
Plinkaigalis, grave 241	-0.2	0.6	-0.2	1.4	0.0	-0.9	-21.5	8.8	0.1	0.72
Turlojiškė, grave 3	-0.8	0.1	-0.1	0.1	-0.7	0.0	-18.5	9.2	0.4	0.05
Average difference	-0.2	0.4	-0.1	0.8	-0.1	-0.4		·		
Stdev	0.7	0.4	0.6	0.9	0.6	0.9				

Table 5. Inter-laboratory comparison of $\delta^{13}C$ and $\delta^{15}N$ bone collagen values and pairwise differences, average values, and standard deviations from the Max Planck Institute (MPI), Northern Arizona University (NAU), and the University of York (UoY)

Figures

Figure 1. Location of study materials

Figure 2. A calibration plot of paired or triplicate ¹⁴C dates for Lithuanian Stone and Bronze Age human remains. Dates by conventional labs are in grey and italicised.

Figure 3. δ^{13} C and δ^{15} N bone collagen values for the same individuals measured at three different laboratories and plotted against the expected consumers' areas with a trophic level shift of approximately 1 ‰ for δ^{13} C and 4.1 ‰ for δ^{15} N. The difference in isotopic values between the wolf and its potential prey was taken as a trophic level shift for nitrogen (for more details see Piličiauskas et al., 2017b). The data for the expected inland fish consumers' area, Latvian stable isotope data from the Subneolithic Riṇṇukalns site, was adapted from Schmölcke et al. (2015), while the other animal data was taken from Lithuanian Subneolithic-Bronze Age sites (see Fig. 4 and Table 4). Grey lines are connecting values of the same individuals.

Figure 4. Human, animal and fish $\delta^{13}C$ and $\delta^{15}N$ bone collagen values from Lithuanian Mesolithic-LBA sites with intra-individual variation of the Biržai CWC single grave in the bottom right corner. Expected consumers' areas are marked by dotted squares with a trophic level shift of approximately 1% for $\delta^{13}C$ and 4.1% for $\delta^{15}N$. The difference in isotopic values between wolf and its potential prey was taken as a trophic level shift for nitrogen (for more details see Piličiauskas et al., 2017b). The data for expected inland fish consumers' area, Latvian stable isotope data from the Subneolithic Riṇṇukalns site, was adapted from Schmölcke et al. (2015), while the other animal data was taken from Lithuanian Subneolithic-Bronze Age sites (see Table 4). 1 – Subneolithic coastal humans from Šventoji 4, 6, 23, 2 – Late Mesolithic-Subneolithic inland humans from Daktariškė 1, Donkalnis, Spiginas, 3 – Neolithic (CWC) humans from Plinkaigalis, Gyvakarai, Biržai, Spiginas, 4 – LBA inland humans from Turlojiškė, 5 – Late Mesolithic infant from Donkalnis, 6 – Neolithic infant from Benaičiai, 7 – wood grouse, 8 – beaver, 9 – auroch/bison, 10 – elk, 11 – red deer, 12 – roe deer, 13 – horse, 14 – boar, 15 – brown bear, 16 – ducks 17 – wolf, 18 – badger, 19 – fox, 20 – pine marten, 21 – dog, 22 – perch, 23 – pikeperch, 24 – pike, 25 – flatfish, 26 – seals (new data; Piličiauskas et al., 2017b; Antanaitis-Jacobs et al., 2009).

Figure 5. Lithuanian human stable isotope data plotted against the other Baltic region data (Fischer et al., 2007; Eriksson, 2004; Piličiauskas et al., 2017b; Tõrv and Meadows, 2015; Antanaitis-Jacobs et al., 2009; Eriksson et al., 2003; Meadows et al., 2016; Reitsema, 2012; Pospieszny et al., 2015; Eriksson and Howcroft, 2014; Laneman, 2012; Laneman and Lang, 2013; Fornander, 2013; Reitsema et al., 2010). 1–4 year old children are excluded in order to avoid data distortion due to breastfeeding. Major subsistence strategies are framed by dashed grey lines.









