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Subsistence strategies of Meshchera lowlands populations during the Eneolithic period – The Bronze Age: Results from a multidisciplinary approach

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ABSTRACT

A multidisciplinary research project was undertaken to investigate the subsistence strategies adopted by populations living in the vicinity of Lake Shagara in the forest zone of Eastern Europe during the Eneolithic period and the Bronze Age. The analyses focused on the graves from the Shagara cemetery located near Lake Shagara. The diets of three populations were investigated: Volosovo (Eneolithic), Shagara 1 (the end of the Middle Bronze Age) and Shagara 2 (the end of the Middle Bronze Age). The latter two belong to the same cultural group (Shagara) but were distinguished in function of their spatial distribution at the Shagara cemetery. The research included archaeological, archaeozoological and stable isotope analyses. Quantitative diet reconstruction relying on human and food isotopic data was performed using the Bayesian mixing model FRUITS.

The isotopic results and the Bayesian analysis showed that the diets of the Volosovo and Shagara 1 populations were relatively similar. These diets relied primarily on terrestrial foods as a source of calories and on terrestrial animals and freshwater fish as a source of protein. Small differences in estimates, albeit not statistically significant, could indicate that for the Shagara 1 population, relative to the Volosovo population, there was an increase in the consumption of plant foods and a lower protein intake. Bayesian estimates for Shagara 2 individuals clearly showed that their main source of calories was terrestrial plants and that these individuals had a comparatively low level of protein intake.

The results obtained in this research demonstrate that there was a shift in subsistence strategies during the Eneolithic period – the Bronze Age transition at Shagara. However, without a more precise local chronology it is not possible to establish if this was a gradual transition or if groups adopting different subsistence strategies coexisted during the Bronze Age. This issue will be addressed in a future radiocarbon dating research programme.

1. Introduction

Food consumption is an essential aspect of any culture and dietary patterns are often associated with adopted economic systems and local environmental conditions. Therefore, diachronic trends in dietary patterns are potential responses to modifications in economic systems and/or adaptations to changing environments. Previous studies of Neolithic and Bronze Age sites in the forest zone of Eastern Europe focused principally on archaeological assemblages (e.g. implements, weapons, and animal bones) as the main source of data for reconstruction of the earliest economic systems. Traditional typological analysis of settlements and burial sites contributed to the reconstruction of mobility patterns and of economic strategies pursued between 4000 and 2000 BCE. Replacement of one culture by a subsequent culture was determined through changes identified in ceramic traditions, processes used to treat flint and bone, and the appearance of new art forms (Krainov, 1987; Timofeev, 2003). However, only a limited number of studies have employed other types of archaeological evidence. These include carbon and nitrogen stable isotope analysis of human remains used to provide insights into the dietary habits of the forest zone populations

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Fig. 1. Location of the Shagara cemetery.

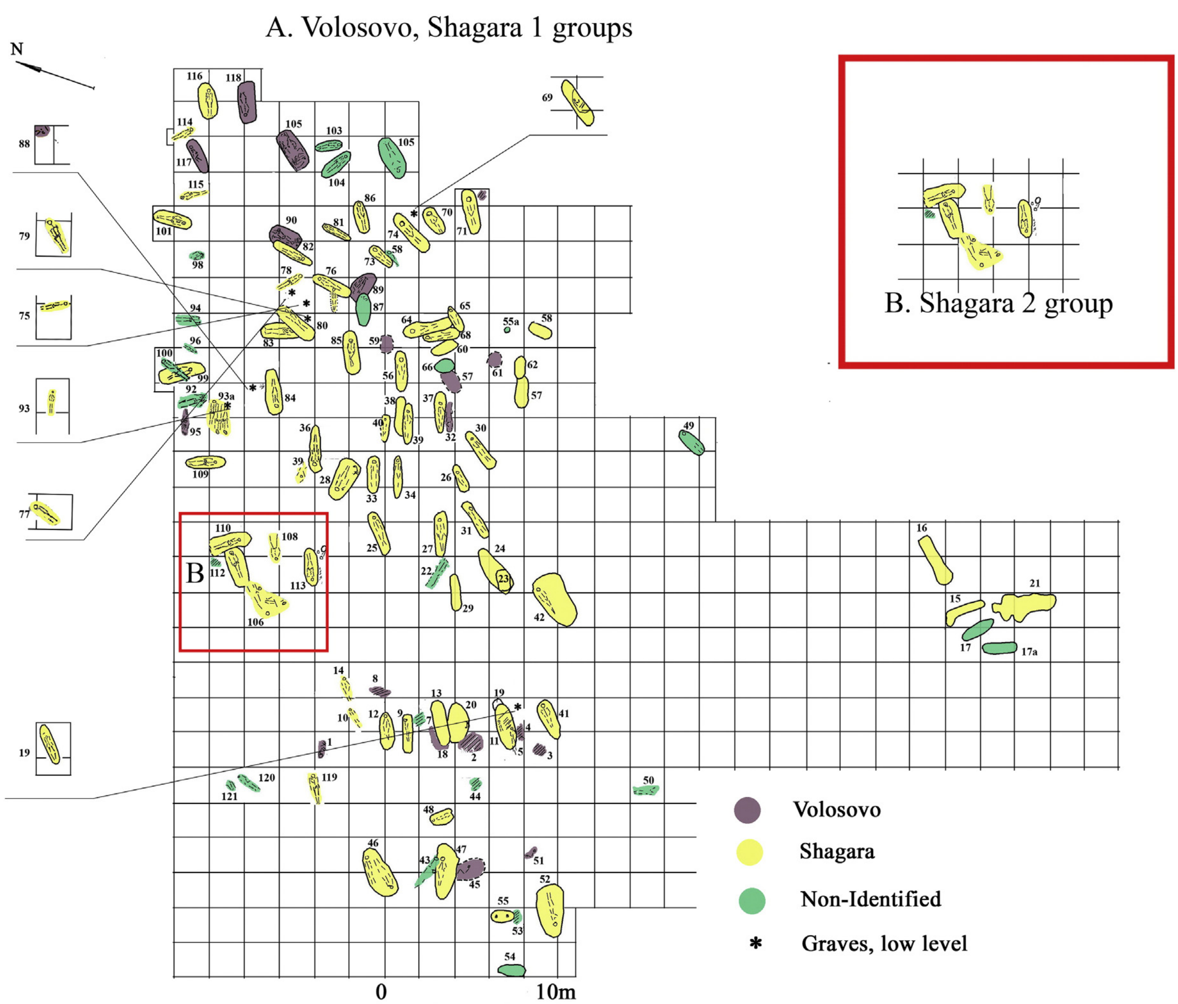

Fig. 2. Plan of the Shagara cemetery.

in the Mesolithic–Eneolithic period (Wood et al., 2013, Fig. 3; Engovatova et al., 2015; Bocherens et al. 2007).

This study aims at investigating diachronic trends in the dietary habits of the populations (Volosovo and Shagara) inhabiting the shores of Lake Shagara (Russian Federation) in the Eneolithic period and at the end of the Middle Bronze Age. An interdisciplinary approach was taken to investigate material remains. It included the study of archaeozoological assemblage. The local carbon and nitrogen isotopic baseline was determined using analysis of archaeological and contemporary food remains. Quantitative diet reconstruction was done using the Bayesian mixing model FRUITS that takes human and food isotopic signatures as data input. The combination of multiple sources of evidence offers a more complete overview of the evolution of the dietary patterns followed by Shagara populations.

2. Cultural context and traditional archaeological studies

2.1. Study area and site description

The Shagara I settlement, containing the Shagara cemetery, is located on the east shore of Lake Shagara (Fig. 1). The site was settled during the Early Neolithic period – the Bronze Age (Kaverzneva, 1992). From the cemetery a total of 121 graves, distributed within an area of ca. 1000 m^2, were examined (Fig. 2). Seven graves were assigned to a lower stratigraphic level, while the remaining 101 graves occupied an upper level. Five burials were located in a separate southern section (Table 1).

Cultural attribution of 113 graves was made on the basis of burial rite and grave offerings (Fig. 3). Two distinct cultural groups were observed, i.e. the Eneolithic Volosovo Culture (3500–2500 BCE) and the Shagara Bronze Age Culture (2000–1800 BCE). Eneolithic Volosovo Culture graves ($n = 26$) were located at the north-eastern and south-western parts of the cemetery at different depth levels (-0.90 to -2.00 m). These were characterized by single and multiple depositions. Bodies were placed lying in an extended posture or on the side in a contracted posture. The bodies were predominantly facing south. Burial offerings included necklaces made from perforated animal teeth and bone pendants shaped as bird heads, amber pendants, and flint (Fig. 4). The Shagara Culture oval graves ($n = 87$) contained skeletons placed in an extended supine posture, and in most cases skulls faced north-east. Two Shagara subgroups were identified based on planigraphy and stratigraphy; graves of subgroup 1 were located evenly across the entire cemetery at different depth levels (-0.80 to -1.7 m), while graves of subgroup 2 formed a cluster in the western part of the cemetery 1.2 m below the surface. Shagara funeral offerings (Fig. 5) included clay vessels, bone and amber implements, amber bronze temple rings, and in one case a clay model of a boat or a cradle (Kaverzneva, 2013).

Table 1
Shagara cemetery. Correlation of stratigraphy (low and upper level) and planigraphy.

Level	Whole area	Southern section
Low level	5 Volosovo graves 2 Shagara 1 graves	–
Upper level	21 Volosovo graves 80 Shagara 1 graves	5 Shagara 2 graves

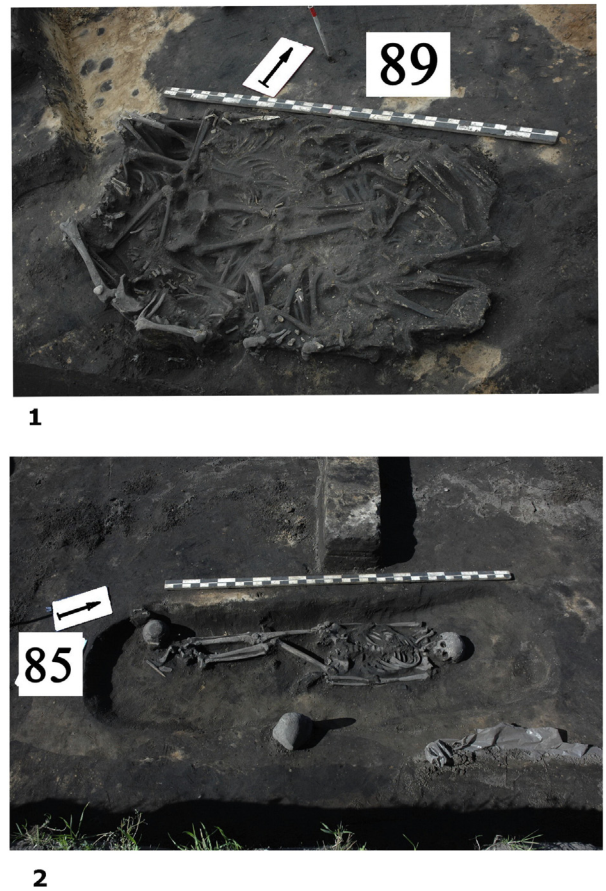

Fig. 3. Shagara cemetery. 1 - Volosovo grave 89; 2 - Shagara grave 85.

3. Materials and methods

3.1. Collagen extraction

Bone collagen was extracted using a modified Longin method (Longin, 1971; Mook and Streurman, 1983).

3.2. Isotope analysis

Stable isotope ratio measurements were made at the GEOKHI RAS, Moscow, Russia, using a DELTA Plus XP isotope mass-spectrometer (ThermoFinnigan), linked to the Flash EA elemental analyser. The isotope ratios are reported in permil notation relative to the international standards VPDB and AIR for $\delta^{13}C$ and $\delta^{15}N$, respectively. Each sample was measured in triplicate and the standard deviation of repeated measurements was 0.2‰ and 0.2 to 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Collagen integrity was assessed the C/N atomic ratio.

3.3. Quantitative diet reconstruction using the Bayesian mixing model FRUITS

The Bayesian mixing model FRUITS (beta 2.0) was used to provide quantitative dietary estimates (Fernandes et al., 2014). The approach taken is similar to that described in two previous cases studies (Fernandes, 2015; Fernandes et al., 2015). These case studies provided highly accurate dietary estimates, established from the comparison of observed and measured dietary contributions. Briefly, the FRUITS model compares human isotope values ($\delta^{15}N_{collagen}$, $\delta^{13}C_{collagen}$) with reference plant, terrestrial animal, and fish food isotope values for the

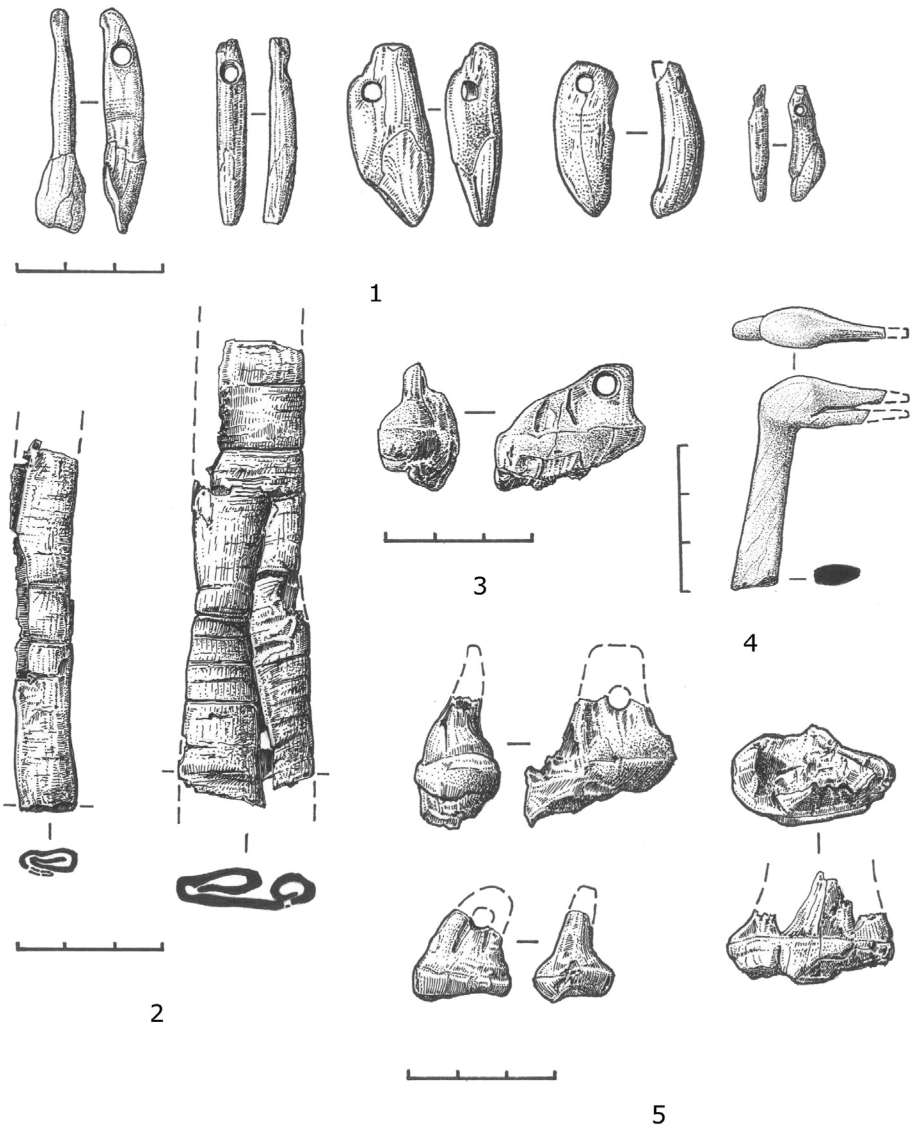

Fig. 4. Shagara cemetery. Volosovo grave offerings: 1, 3, 5 – pendants made of animal perforated teeth, grave 18; 2 – birch-bark bob, cultural layer; 4 – bone figurine, grave 18.

study area (Table 1). Three food groups were defined (C3 plants, terrestrial herbivores, and freshwater fish). To define plant reference values only modern samples were available and isotopic measurements showed the presence of isotopic values considerably higher than those expected for pre-historic samples (Richards and Trinkaus, 2009). Thus only plants with $\delta\ ^{15}N$ values below 4‰ were taken as reference. Terrestrial plants pre-industrial $\delta^{13}C$ values are corrected by adding a constant value of 1.5‰, as adopted in previous studies (Dewar and Pfeiffer, 2010). The isotopic offsets between measured (e.g. collagen) and edible fractions (protein, lipids, carbohydrates), plus macronutrient compositions were established following previous references (Fernandes, 2015; Fernandes et al., 2015). The previous references also describe employed diet-to-tissue isotopic offsets. In the case of collagen carbon, a routed model was employed that accounts for the dietary contributions from lipids and carbohydrates towards bone collagen (Fernandes et al., 2012). For the different model parameters, including for isotopic values in individual consumers, conservative uncertainties were taken as the reference. Finally, to constrain model estimates a purely physiological prior was introduced limiting protein intake to acceptable levels between 10 and 35% of total calories (Otten et al., 2006). The default FRUITS model is given as Supplementary material. Assessment of model convergence and tests to the robustness of generated estimates are presented in Supplementary file 3.

4. Results

4.1. Archaeozoological analyses

Bones of mammals and fish were recovered from settlement occupation layers and graves (Supplementary file 1, Table 1). As the settlement was occupied for several millennia, and subsequently a cemetery appeared on the same territory, the stratigraphic sequence of the layers was disturbed. Nevertheless the distribution of the funeral offerings offers a possibility to attribute the lower layers (9–5) to the Volosovo Eneolithic culture whereas the upper layers (4–1) are attributed the Bronze Age Shagara culture. Bones of undomesticated animals were predominant (98.6%). These were found in all settlement layers, with three quarters of the remains recovered from layers 4, 5, and 6. Elk (47.8%), beaver (12.0%), and bird (18.1%) bones make up the bulk of the bone finds. Analysis of fish bones showed that pike accounts for the largest share of finds in the cemetery and at the settlement (Supplementary material, Tables 2 and 3). Hence, hunting and fishing were key

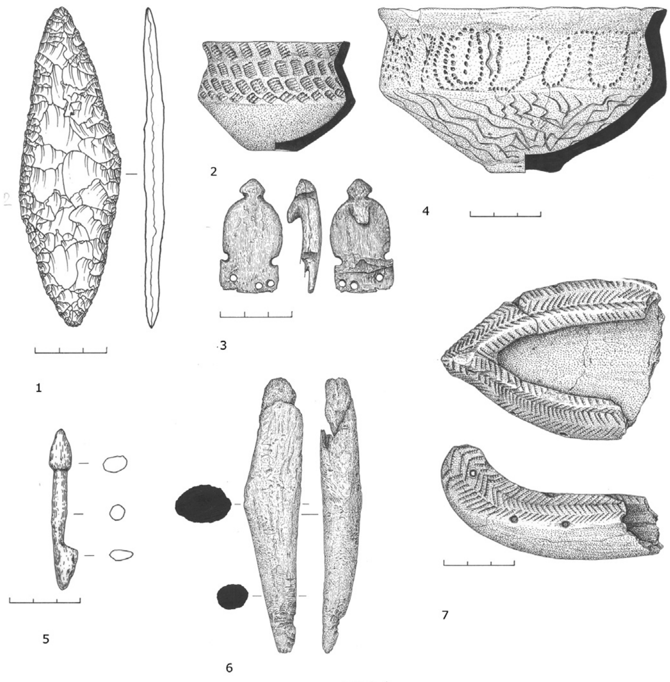

Fig. 5. Shagara cemetery. Shagara grave offerings: 1 – flint dagger, grave 113; 2 – clay vessels, grave 93a; 3 – bone zoomorphic belt-clasp, grave 52; 5 – bone harpoon, grave 9; 6 – bone hoe (?), grave 106; 7 – clay model of boat, grave 93a.

subsistence activities throughout the occupation period of the settlement. However, it was difficult to estimate the percentage share of plant components in the dietary system based on these data. Furthermore, it was not clear from the archaeological evidence whether there were any differences in the dietary systems of the Volosovo and the Shagara groups.

4.2. Stable isotope analyses

In general, collagen preservation conditions were good with bone atomic C/N ratios ranging between 3.2 and 3.4 collagen (DeNiro, 1985; Ambrose, 1990). However, some animal bones from layers 4, 5 and 6, as well as human bones from several graves, did not preserve collagen. These samples were excluded from the analyses.

4.3. Isotopic signatures of food groups

Bone samples of herbivores, omnivores, fish bones and other aquatic animals selected from different settlement and cemetery occupation layers were subjected to isotopic analysis. Contemporary water plants and terrestrial plants were also analyzed (Table 2; Fig. 6).

4.4. Isotopic signatures in human bone collagen

Bone samples from 19 Volosovo and 29 Shagara individuals were subjected to isotope analysis (Table 3, Fig. 6). Isotope values of the two Shagara subgroups (1 and 2) are listed separately (see Study area and site description).

4.4.1. Dietary estimates generated by FRUITS

The dietary estimates generated by the FRUITS model are expressed as relative calorie (%) contributions. These estimates are represented in Table 4 and evaluate the caloric contributions from each food group (also represented in Fig. 7), the relative protein contribution from each food group, and finally the dietary protein contribution. This latter estimate indicates the proportion of protein in the diet relative to total macronutrient intake (protein, carbohydrates, and lipids). Model performance tests showed that model convergence was reasonable and that estimates were robust to small changes in model parameters (Supplementary file 3).

Estimate uncertainties were between 10 and 20% and in the case of Volosovo 1 and Shagara subgroup 1 the estimated calorie contributions from plant and terrestrial animal foods overlap considerably. Thus, under this level of uncertainty some caution is necessary in the interpretation of the results. Nonetheless, average model estimates do suggest differences in dietary preferences among the different population

Table 2
Shagara foodweb isotope values.

Sample/species	Bone	$\delta^{13}C$ (‰) VPDB	$\delta^{15}N$ (‰) AIR	C/N	Location
Archaeological samples					
Terrestrial herbivores (#23 samples)					
Elk	Tubular	−23.0	+4.5	3.3	Layer 1
Elk	Tubular	−22.3	+4.2	3.2	Layer 2
Elk	Tubular	−22.7	+4.2	3.2	Layer 2
Elk	Tubular	−22.7	+4.1	3.2	Layer 3
Cattle	Tubular	−22.3	+7.0	3.3	Layer 4
Cattle	Tubular	−20.2	+6.1	3.3	Layer 4
Cattle	Tubular	−26.1	+6.0	3.3	Layer 4
Cattle	Phalange	−20.9	+6.0	3.3	Layer 4
Cattle	Tubular	−26.1	+6.0	3.3	Layer 4
Elk	Astragalus	−23.2	+4.7	3,1	Layer 4
Sheep/goat	Tubular	−21.3	+5.4	3.3	Layer 6
Elk	Metapodium	−22.7	+4.2	3.3	Layer 6
Wild boar	Radial	−21.9	+7.5	3.3	Layer 7
Wild boar	Fang	−21.9	+7.5	3.3	Layer 7
Bear	Ulna	−21.0	+6.1	3.2	Layer 7
Bear	Tubular	−20.6	+6.1	3.2	Layer 7
Elk	Metapodium	−22.1	+4.2	3.0	Layer 7
Beaver	Tubular	−25.6	+11.5	3.2	Layer 8
Elk	Astragalus	−22.7	+4.3	3.3	Layer 8
Elk	Phalange	−23.0	+4.5	3.3	Layer 9
Bear	Fang	−20.0	+6.0	3.3	Layer 9
Bear	Tubular	−20.1	+6.0	3.3	Layer 9
Terrestrial carnivores					
Marten	Tubular	−18.6	+9.8	3.3	Layer 9
Freshwater fauna (#16 samples)					
Tench	Vertebra	−27.9	+9.2	3.2	Grave
Carp	Cleitrum	−25.7	+8.2	3.2	Layer 4
Pike	Dentale	−25.9	+10.4	3.2	Layer 5
Ide	Rib	−27.2	+8.6	3,1	Layer 5
Pike	Dentale	−24.4	+10.9	3.3	Layer 6
Pike	Dentale	−25.0	+12.1	3.3	Layer 6
Pike	Dentale	−23.7	+10.4	3.3	Layer 6
Ide	Cleitrum	−25.9	+11.8	3.3	Layer 6
Fish	–	−25.6	+10.5	3.3	Layer 6
Catfish	Fin	−24.4	+9.9	3.3	Layer 8
Pike	Dentale	−24.5	+9.5	3.2	Layer 8
Crucian carp	–	−25.5	+9.0	3.2	Layer 8
Pike	Preoperculare	−25.6	+11.6	3.3	Layer 9
Pike	Cleitrum	−25.5	+9.8	3.3	Layer 9
Fish scales	–	−24.7	+8.2	3.3	Occupation layer
Tortoise	Shell	−25.0	+10.4	3.3	Occupation layer
Contemporary samples					
Terrestrial plant samples Lake Shagara shore (#9 samples)					
Artemisia	–	−27.4	+2.0	–	–
Artemisia	–	−28.9	+6.5	–	–
Reed mace	–	−28.4	−2.0	–	–
Reed mace	–	−27.4	+1.0	–	–
Plants and reed	–	−28.6	+3.0	–	–
Reed mace	–	−27.5	+1.5	–	–
Wild gramineous plants	–	−26.6	+9.2	–	–
Wild gramineous plants	–	−26.6	+4.5	–	–
Wild gramineous plants	–	−26.8	+8.3	–	–

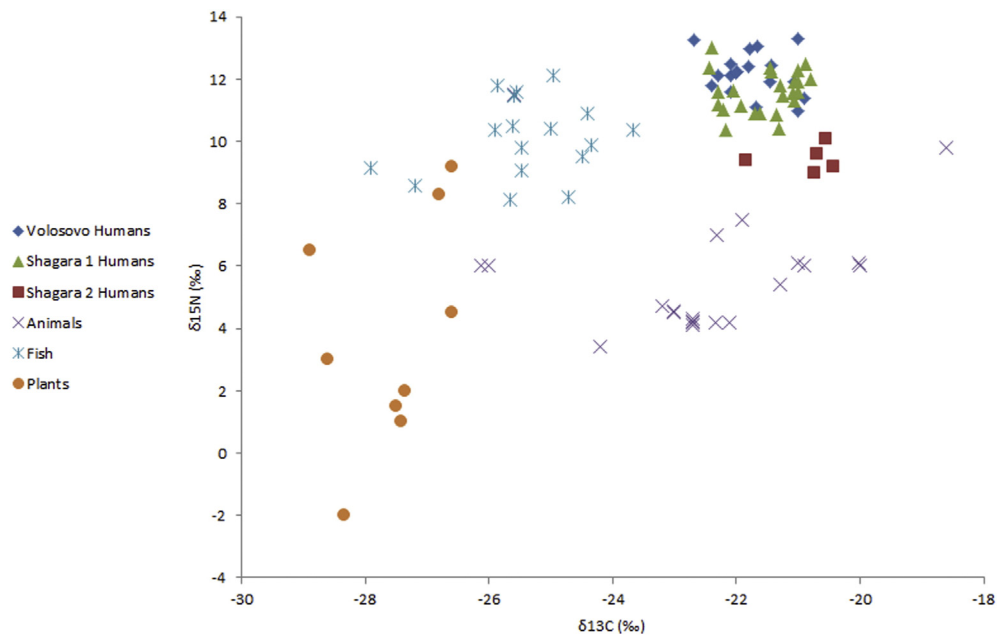

Fig. 6. Nitrogen and carbon stable isotope distribution plotted for Volosovo and Shagara humans, animals and fish from Shagara cemetery and contemporary plant samples.

groups. The Volosovo group relied primarily on terrestrial foods as a calorie source (ca. 90%). However, model estimates clearly show that animal food sources (terrestrial herbivores and fish) represented the major source of dietary protein for the Volosovo group (ca. 75%). This significant dependence on animal protein and the estimated high protein intake (ca. 23%) approaches the dietary preferences observed in some hunter-gatherer diets (Cordain et al., 2000). Shagara 1 subgroup a dietary pattern similar to that observed for the Volosovo group. Shagara 1 subgroup also shows a predominant dependence on animal protein (ca. 70%) and a relatively high protein intake (ca. 21%). The average values for plant calorie contributions are slightly higher compared with Volosovo but as mentioned previously some caution is needed in the interpretation of these results given the relatively large uncertainties. However, the dietary preferences of Shagara 2 subgroup contrast significantly with those of the Shagara 1 subgroup and the Volosovo group. The major calorie contributions for Shagara 2 subgroup are markedly plant foods (ca. 83%) and these represent also the main source of dietary protein (ca. 62%). The estimated level of protein intake (ca. 15%) is similar to that observed in modern Western populations that rely predominately on carbohydrates as a calorie source (Lands et al., 1990).

4.4.2. Discussion

Comprehensive archaeological, archaeozoological and isotope analyses were employed in the study of the dietary patterns of the population groups that lived near Lake Shagara during the Eneolithic period and the end of the Middle Bronze Age.

The isotopic signatures recorded in the bone collagen of Volosovo and Shagara subgroup 1 individuals indicate that the dietary preferences of these two populations were similar. This is confirmed by the estimates of the dietary contributions from each food group made by the FRUITS model, which clearly shows that animal protein was the main source of dietary protein. However, the estimated average contributions also suggest a slight increase in the dependence on plant foods by the Shagara 1 population compared to the Volosovo population. The interpretation of this difference requires some caution given the relatively large model uncertainties, nonetheless it may be explained by differences in the economic systems. Hunting was a key economic activity of both the Volosovo and Shagara subgroup 1 populations. While gathering of plants and fishing were secondary economic activities. This is attested by the presence of archaeological artifacts such as arrowheads, fishing hooks, harpoons, and impressions of nets and floaters. This combined archaeological information suggests that throughout several centuries of the Eneolithic period and at the end of the Middle Bronze Age (4000–2000 BCE) hunting-gathering represented the prevailing economic strategy of forest populations.

However, the presence of bones from domesticated animals in the middle and upper archaeological layers suggests a gradual penetration of food-producing skills into the forest zone or arrival of a population group that had developed a new economic system. This statement is consistent with the overall assessment of the historical and paleoecological situation (Klimanov, 1986; Aleshinskaya, 1999) in the forest zone of Eastern Europe which saw the arrival of different population groups at the end of 3000 BCE (Kaverzneva, 1992). Possibly, the newcomers introduced domesticated animals and plants. Therefore, a follow-up study should include radiocarbon dating of domesticated animal bones from the Shagara settlement layers to establish the chronology of their introduction. The dietary pattern of the Shagara subgroup 2 was significantly different from that of the Volosovo population and Shagara subgroup 1. For the individuals attributed to Shagara subgroup 2 the estimates generated using FRUITS indicate that the main source of calories was plant carbohydrates. A horn implement, supposedly, a hoe, was found in one of the Shagara subgroup 2 graves. If Shagara subgroups 1 and 2 are contemporary this could indicate that a small group of individuals was engaged in the collection and cooking of wild plants. Alternatively, Shagara subgroup 2 individuals may also correspond to a later time period when the dietary dependence on domesticated animals and plants was more intensive. Thus, a follow-up study should also include human radiocarbon dates to verify if the individuals from the Shagara subgroup 2 may be assigned to a later time period. Nevertheless, appearance of a group within the Shagara population with a dietary intake different from the diet of the preceding Volosovo population and Shagara subgroup 1 population implies that at the turn of 3000 BCE a new mode of subsistence was being adopted. Gradually, some groups shifted their subsistence strategy from hunting-gathering to the production of domesticated animals and plants.

Table 3
Shagara Cemetery. Data on $\delta^{15}N$ and $\delta^{13}C$ in the Bone Collagen of Buried Individuals.

Sample	Sex/Age	Bone type	$\delta^{13}C$, ‰ VPDB	$\delta^{15}N$, ‰ AIR	C/N
VOLOSOVO GROUP (#19 samples)					
Grave 8, skeleton	Male 25–35	Femur	−21.7	+11.1	3.3
Grave 18, skeleton 1	Female 25–35	Femur	−21.1	+11.9	3.3
Grave 18, skeleton 2	Juvenile 14–15	Femur	−21.4	+12.4	3.3
Grave 18, skeleton 3	Juvenile 15?	Femur	−21.8	+12.4	3.3
Grave 18, skeleton 4	Child 9–10	Femur	−21.4	+11.9	3.2
Grave 18, skeleton 5	Child	Femur	−21.0	+13.3	3.2
Grave 18, skeleton 6	Male 35–45	Femur	−22.1	+12.5	3.1
Grave 37, skeleton	Male 35–45	Femur	−22.1	+11.6	3.3
Grave 51, skeleton	Child 7–8	Femur	−22.1	+12.1	3.3
Grave 89, skeleton 1	Adult	Femur	−22.0	+12.2	3.3
Grave 89, skeleton 3	Adult	Toe bone	−22.7	+13.2	3.2
Grave 89, skeleton 7	Male? Adult	Tone bone	−22.4	+11.8	3.2
Grave 89, skeleton 8	Male 30–40	Finger bone	−21.8	+13.0	3.2
Grave 89, skeleton 12	Child	Femur	−21.7	+13.1	3.3
Grave 95, skeleton	Female 40–50	Femur	−21.0	+11.0	3.3
Grave 99, skeleton	Female 25–35	Femur	−22.0	+12.2	3.3
Grave 110, skeleton	Female 35–45	Femur	−20.9	+11.4	3.1
Grave 111, skeleton	Female 25–35	Femur	−20.8	+11.3	3.2
Grave 117, skeleton	Child 11–13	Femur	−22.3	+12.1	3.2
SHAGARA GROUP					
Subgroup 1 (# 24 samples)					
Grave 5, skeleton	Female, adult	Femur	−22.0	+11.6	3.3
Grave 10, skeleton	Male 15–25	Femur	−21.1	+11.9	3.3
Grave 11, skeleton	Juvenile 14–15	Femur	−22.2	+10.4	3.3
Grave 13, skeleton	Female 35–45	Femur	−21.2	+11.5	3.2
Grave 14, skeleton	Male 35–45	Rib	−22.0	+11.2	3.2
Grave 39, skeleton	Male 35–45	Femur	−22.3	+11.9	3.3
Grave 52, skeleton	Male 20–30	Rib	−21.0	+12.3	3.2
Grave 76, skeleton 1	Female 30–40	Femur	−21.4	+10.9	3.3
Grave 77, skeleton	Female 30–40	Femur	−22.2	+11.0	3.3
Grave 78, skeleton	Female 35–45	Femur	−21.6	+10.9	3.3
Grave 79, skeleton	Adult?	Rib	−22.3	+11.6	3.2
Grave 80, skeleton	Female 25–35	Femur	−21.4	+12.3	3.2
Grave 82, skeleton	Female 25–35	Femur	−22.4	+12.4	3.1
Grave 83, skeleton	Male 30–40	Femur	−21.1	+11.6	3.1
Grave 84, skeleton	Male 30–40	Femur	−20.9	+12.5	3.1
Grave 85, skeleton	Female 25–35	Femur	−21.5	+12.4	3.1
Grave 93a, skeleton 1	Male 45–55	Femur	−21.0	+11.6	3.2
Grave 93a, skeleton 3	Female 50–60	Femur	−21.7	+10.9	3.2
Grave 93a, skeleton 2	Male 25–35	Femur	−21.0	+11.9	3.2
Grave 101, skeleton	Female 30–40	Femur	−22.4	+13.0	3.2
Grave 107 skeleton	Male 30–40	Femur	−21.1	+11.3	3.2
Grave 108 skeleton	Male 30–40	Femur	−21.6	+11.8	3.2
Grave 109, skeleton	Male 30–40	Toe finger	−21.3	+10.4	3.2
Grave 116, skeleton 4	Male 35–45	Femur	−20.8	+12.0	3.3
Subgroup 2 (# 5 samples)					
Grave 106, skeleton 1	Juvenile, 12–13	Femur	−20.7	+9.6	3.3
Grave 106, skeleton 2	Male 25–35	Femur	−20.4	+9.2	3.3
Grave 106, skeleton 3	Female 25–35	Femur	−20.6	+10.1	3.2
Grave 110, skeleton	Female 35–45	Femur	−20.7	+9.0	3.1
Grave 113, skeleton	Male 30–40	Femur	−21.9	+9.4	3.0

Average isotopic values of the Volosovo Eneolithic group ($\delta^{13}C = -21.7‰$, $\delta^{15}N = +12.1‰$) were similar to those observed for the Bronze Age Shagara subgroup 1 ($\delta^{13}C = -21.5‰$, $\delta^{15}N = +11.6‰$). However, the smaller Bronze Age Shagara subgroup 2 showed a significantly different average isotopic signature ($\delta^{13}C = -20.9‰$, $\delta^{15}N = +9.3‰$).

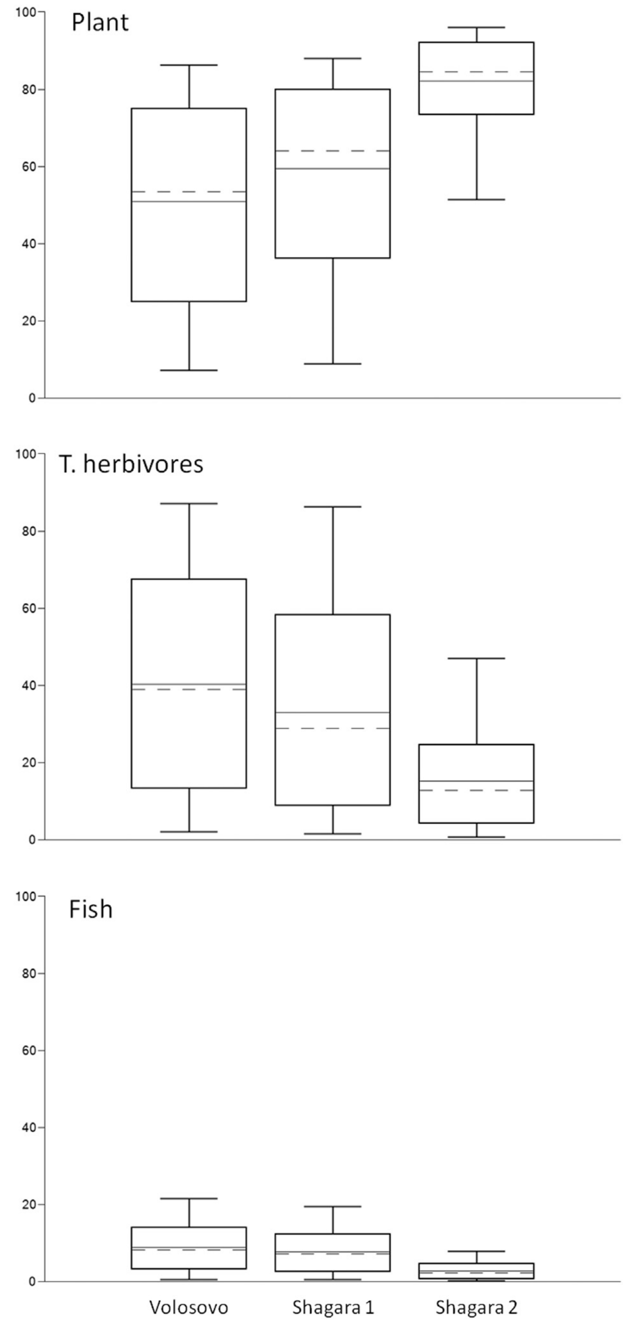

Fig. 7. Credible intervals of estimated calorie intake for different population groups. Boxes represent a 68% credible interval (corresponding to the 16th and 84th percentiles) while the whiskers represent a 95% credible interval (corresponding to the 2.5th and 97.5th percentiles). The horizontal continuous line represents the estimated mean while the horizontal discontinuous line represents the estimated median (50th percentile).

5. Conclusions

Comprehensive archaeological, archaeozoological and isotope analyses were employed to investigate the subsistence strategies followed by populations living in the vicinity of Lake Shagara in the forest zone of Eastern Europe during the Eneolithic period and the Bronze Age. The subsistence strategies adopted by Volosovo and Shagara subgroup 1 populations were similar. For these groups, the outcome of the

Table 4
Dietary estimates expressed as relative calorie (%) contributions from each food group, food group protein, and dietary protein.

Group/subgroup	T. plants (cal %)	T. herbivores (cal %)	Fish (cal %)	Plant protein (cal %)	T. herbivores protein (cal %)	Fish protein (cal %)	Protein (cal %)
Volosovo	50 ± 22	41 ± 24	9 ± 5	25 ± 15	50 ± 25	25 ± 14	23 ± 5
Shagara 1	56 ± 22	37 ± 24	7 ± 4	30 ± 16	49 ± 25	21 ± 13	21 ± 5
Shagara 2	83 ± 10	14 ± 11	3 ± 2	62 ± 14	26 ± 17	13 ± 9	15 ± 3

Bayesian analysis demonstrated that the main sources of protein were herbivores and fish. The main sources of calories were terrestrial foods, however, due to large uncertainties in estimates it was not possible to distinguish between the caloric contributions from terrestrial plants and terrestrial herbivores. Nonetheless, the average values of estimates do suggest an increase in the dependence of plant foods and a lower level of protein in the diet for Shagara subgroup 1 populations compared to Volosovo populations. This could mark the onset of a shift in economic systems as observed from the archaeozoological data that shows an increase in the use of domesticated animals. It is likely that this difference was caused by climatic changes. Furthermore, the Shagara subgroup 2 adopted a subsistence strategy that clearly contrasted with those of Shagara subgroup 1 and Volosovo populations. The outcome of the Bayesian analysis showed that Shagara subgroup 2 individuals had as their main source of calories plant foods and a relatively low level of protein intake. Future research, that will include radiocarbon measurements, will aim at establishing the chronologies of the different populations. A main research aim will be to investigate if the two types of subsistence strategies observed for Shagara populations coexisted or if these correspond to a gradual shift.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jasrep.2016.08.043.

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