

APPROACHES TO DETERMINE RESERVOIR EFFECTS IN ELK/MOOSE

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ABSTRACT. The elk/moose (*Alces alces*) was an important resource for prehistoric societies. In prehistoric art, it is often depicted in connection with water. Biologists find that elk spend much time in water and consume considerable amounts of aquatic plants. As freshwater plants can have reservoir ages of hundreds or even thousands of years, there is a risk of a significant reservoir effect in elk bones and antler, and artifacts made of these materials. This pilot study followed several approaches to investigate the possibility of a freshwater reservoir effect in elk. I analyzed modern, historical and archaeological bones and antler from several sites across Eurasia. Skull bone and antler of the same individual were radiocarbon dated, as antler is formed in summer, when the proportion of aquatic diet is supposed to be highest. Age offsets measured in this study were zero to about 500 years. A difference between bone and antler could not be determined. The reservoir effect appears to be smaller than estimated from accounts of elk diet, even in regions where a substantial freshwater reservoir effect is expected. Therefore, the hypothesis of a large proportion of aquatic diet can be rejected for several of the individuals studied here.

KEYWORDS: elk, freshwater, moose, reservoir effect.

INTRODUCTION

Accurate radiocarbon dating of the remains of European elk (or moose, *Alces alces*, in the following called “elk”) is important for prehistoric archaeology as this species was an important resource throughout prehistory. In Northern Europe, the Baltic region and Northern Russia, elk were a common game animal, especially during the Late Palaeolithic/Allerød. Elk seem to disappear during the Younger Dryas but invade with the beginning of the Holocene (Degerbøl 1939, 1964; Bokelmann 1978; Terberger 2006; Aaris-Sørensen 2009; Riede et al. 2010; Larsson 2015). Elk remains dominated the fauna assemblages in some regions, especially in northeast Europe (e.g. Degerbøl 1964; Gumiński 1998; Timofeev 1998; Zhilin 2006). In other regions, they were less numerous, but still present (Richter 1991). Elk bones and antlers were often used to produce tools (e.g. Gramsch 1973 and references therein; Møller Hansen and Buck Pedersen 2006; Larsson 2015). However, elk were not only important for economic reasons. They are often represented in Northern European Late Palaeolithic/Mesolithic art (e.g. Zaliznyak 1998; Kabaciński et al. 2011). Even at sites where elk bones do not dominate the animal remains, depictions such as figurines have been found (e.g. Iršėnas 2000). The significance of elk therefore exceeds the purely economic needs.

In the North European Plain and the Western Baltic, the elk was a key element in Late Palaeolithic/Early Mesolithic art and rituals (Mathiassen 1953; Sørensen 1978; Møller Hansen and Buck Pedersen 2006; Terberger 2006; Kabaciński et al. 2011; Veil et al. 2012; Jessen et al. 2015). With the development of dense forests, elk populations declined in parts of that region and the elk lost first its economic and later its symbolic significance (Andersen et al. 1990; Kabaciński et al. 2011). Further to the north and east, however, elk populations continued to exist, and so did the economic and symbolic importance of the elk.

In Fennoscandia and Eastern Europe to the Eastern Urals, elk and especially elk head depictions are common from the 6th millennium BC until about 1000 BC (Carpelan 1975; Iršėnas 2000; Bradley et al. 2001; Zhulnikov and Koshina 2010). Elk representations are

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made from a wide variety of materials and occur on staffs, boat prows, skis, axes, knives and spoons, as figurines and pendants and in rock art (Carpelan 1975; Singleton 1989, 1998; Iršénas 2000; Loze 2010; Kashina and Zhulnikov 2011). The importance of the elk is further illustrated by artifacts and grave goods made of elk teeth, antler and bone (e.g. Butrimas and Jankauskas 1998; Zhilin 2010; Płonka et al. 2011). For example, these were imported to the island of Zealand, Denmark, even after elk had become extinct there (Aaris-Sørensen 1985; Schmölcke and Zachos 2005). Accurate radiocarbon dating of elk remains is thus crucial as they represent an important part of prehistoric economy and symbolism.

Many depictions show elk in combination with water. For example, boats with elk heads are common in Scandinavian rock art (e.g. Singleton 1989, 1998; Helskog 2014; Sapwell 2014). At Lehtajärvi, northwest of Rovaniemi in Finnish Lapland, an elk head carved in pine had been found. It is ^{14}C -dated to about 5800 BC and “appears to be the prow of a boat” (Singleton 1989, 1998). It is suggested that the elk, similar to seals or boats, can be regarded as a liminal agent, at home both in the water and on land (Helskog 2004; Westerdahl 2005). Today, it is impossible to tell whether boats with elk heads show actual boats, either decorated or camouflaged for elk hunting, or whether they are pictorial transitions between elks and boats (Westerdahl 2005). In any case, observations of elks swimming in the water must have been common in prehistory (Westerdahl 2005), as supported by modern studies of elk behavior.

During summer, elk spend a lot of time in or near the water (Peterson 1955; Corbet 1966; Lenarz et al. 2011). Numerous reasons have been proposed: elk need to cool down during hot summer days; they can escape biting flies in the water; and they consume aquatic plants (Peek 1998). The latter has been suggested to be the most important reason for the elk spending so much time in the water, e.g., because of the high sodium content of the aquatic plants (Runtz 1991; Peek 1998). This is supported by the fact that aquatic feeding begins before the appearance of large flies and that moose observed in water were feeding or standing with parts of their body exposed to insect attack (Peek 1998). Elk are not limited to floating or emerging plants, as they have been reported to uproot plants from water depths of up to five metres and consume them while totally submerged (Runtz 1991; Geist 1999). In general, a wide variety of aquatic species is targeted by elk, including *Nymphaeaceae*, *Potamogetonaceae* and *Typhaeaceae* (Renecker and Schwartz 1998: 418–419, tab. 36). The higher contents of crude protein and gross energy in aquatic plants, when adjusted for digestibility, outweigh the increased energy cost of locomotion in water and ingestion of water during feeding (Peek 1998). Even if this had not been the case, the cooling effect of the water could outweigh a lower energy return from aquatic plants (Renecker and Schwartz 1998). It has been suggested that during summer, up to 50% of the elk’s diet consist of aquatic plants (Burton 1998). However, this study and other quantitative investigations conclude that this might be overestimated in many cases (see the Discussion section).

The potentially high proportion of aquatic diet is a concern for radiocarbon dating. The freshwater reservoir effect can be very high and variable (Keaveney and Reimer 2012; Philippsen 2013; Philippsen and Heinemeier 2013) and can thus be a significant source of error when radiocarbon dating elk remains.

This project presented here is a pilot study, based on funding for only 20 radiocarbon dates. With the limited amount of samples that were possible to date in this study, I tried to cover as

many different approaches as possible. I aim at using the information gained from this study in later projects with greater numbers of samples. In this study, I radiocarbon date different elk remains with known age or associated terrestrial samples. Antler and skull bone of the same individual are dated, as antlers form during summer, when the proportion of aquatic diet is assumed to be largest. The antler would thus have a higher reservoir age than the bone.

SITES AND SAMPLES

Samples of elk bone and antler with known age or other forms of independent age control were chosen. Three historical elks were obtained from Norway, while most samples derive from Early Holocene archaeological contexts across Eurasia.

From Norway, three historical known-age, pre-bomb elk bones were acquired from Melhus, Selbu, and Bratsberg (Figure 1), all situated within an area with calcareous lakes. An aquatic plant from Melhus was collected in May 2015 to check for the freshwater reservoir effect. A sample of elk feces was collected in summer 2015 in Siberia, Russia, as it is an example of the elk's diet in summer.

From the Preboreal-Boreal peat bog site Stanovoye 4 in the Upper Volga area, Russia, I received two elk antler artifacts from which wooden handles had already been ¹⁴C-dated (Hartz et al. 2010). Here, the elk antler artifacts themselves were dated.

From the excavation FHM4096 at Aldersro, Denmark, a twig of yew/juniper (find no. x4705) was found right next to an elk antler and bone (find no. x4701) in a former dead ice lake. The twig and antler are assumed to be contemporaneous (pers. comm. Henrik Skousen and Uffe Rasmussen).

Four collagen samples from Friesack 27 (Groß 2014) were provided by Charlotte Hegge, Kiel University. From two layer complexes, we have a pair of elk and terrestrial animal. The finds within one layer complex are assumed to be contemporaneous.

Beregovaya II, layer 2 comprises an Early Neolithic layer at the Gorbunovo peat bog, Russia. Layer 2 is embedded in peat and was dated to the Early Atlantic by pollen analysis and radiocarbon dated to about 7300 BP. In this study, two elk bones and two reindeer bones which are assumed to be contemporaneous were dated.

From the site "Tuehuset", Em Sogn, Børglum Herred, Denmark, Per Lysdahl provided a sample of elk antler with some skull bone remains still attached to it. This sample pair will show if there is any difference in the radiocarbon age of summer diet (antler) vs. total diet (bone).

METHODS

Bone and antler samples were demineralised with 1M HCl at 4°C over several days, until effervescence ceased (complete dissolution of calcium carbonate) and no density gradient was observed (complete dissolution of calcium phosphate). Humates were removed with 0.1M NaOH, with renewed NaOH until the solution remained colorless; each base step lasted several hours at 4°C. After each acid or base step, the samples were rinsed 3 times with dem. H₂O. Lastly, the samples were rinsed three times with a weak HCl solution (pH = 2), covered with that solution, and heated to 58–80°C for 48 hr, until the collagen was dissolved. The samples were centrifuged (15 min @ 2000 rpm) and filtered through

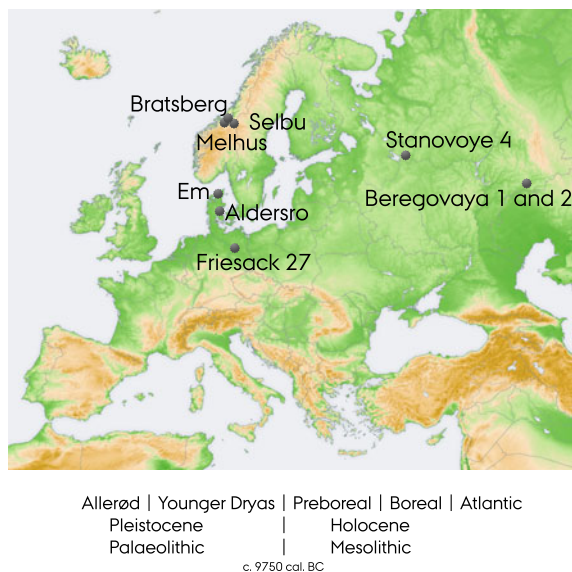


Figure 1 Map indicating the locations from where the samples originate. Background map: in the public domain, created by <https://commons.wikimedia.org> user San Jose. The insert shows the order of the environmental, climatic, and cultural phases mentioned in the text (based on the nomenclature commonly used in Denmark).

0.45- μm syringe filters, before they were freeze-dried. The collagen samples from Friesack were prepared with a modified Longin method at Kiel University. Radiocarbon dates were measured on the AMS systems of the Aarhus AMS Centre and at Direct AMS, Seattle USA, with data analysis and quality control in Aarhus. Stable isotopes were measured using a continuous-flow IsoPrime IRMS coupled to an elemental analyzer at the Aarhus AMS Centre.

RESULTS

The radiocarbon dates and stable isotope measurements are presented in Table 1. Figures 2, 3, and 4 display the calibrated radiocarbon ages for the Norwegian sites; Em, Friesack 27 and Stanovoye 4; and Beregovaya 2. The samples were calibrated in OxCal 4.2.4 (Bronk Ramsey 2009; Ramsey and Lee 2013) using the terrestrial calibration curve IntCal13 (Reimer et al. 2013).

The stable isotope values measured on elk bone and antler range from -24.94 to -18.79‰ (Table 1). The average is -21.64‰ , with a standard deviation of 1.43‰ . The $\delta^{15}\text{N}$ range is even larger, from 2.11 to 9.90‰ , with an average of 4.24 and standard deviation of 2.00‰ . The isotope values of the elk samples do not differ significantly from the bones of other animals of the same site, such as the roe deer and wild boar at Friesack or the reindeer at Beregovaya (Table 1).

The historical elks from Norway died between AD 1898 and 1925. Their radiocarbon ages can be compared to the radiocarbon age of the contemporaneous atmosphere, as provided by

Table 1 Radiocarbon and stable isotope measurements of the samples discussed in this study.

AAR	Site	Species	Material	Comments	¹⁴ C age (pMC)	δ ¹³ C (‰ VPDB)	δ ¹⁵ N (‰ AIR)	C:N ratio	C %	N %
21979	Selbu, Norway	Elk (<i>Alces alces</i>)	Antler	AD 1925. IntCal: 132 ± 6 BP	80 ± 25	-21.95	2.45	3.17	38.87	14.30
21980	Melhus, Norway	Elk (<i>Alces alces</i>)	Bone	AD 1898. IntCal: 73 ± 7 BP	112 ± 25	-22.00	2.11	3.31	41.14	14.49
21981	Bratsberg, Norway	Elk (<i>Alces alces</i>)	Bone	AD 1914. IntCal: 105 ± 7 BP	172 ± 25	-22.37	2.12	3.23	43.57	15.76
23140	Melhus, Norway	Pondweed (<i>Potamogeton natans</i>)	Plant	AD 2015. Reservoir age estimate 219 ± 32 ¹⁴ C yr.	pMC 101.41 ± 0.41	N/A	6.31	45.54	46.20	1.22
28137	Siberia, Russia	Elk (<i>Alces alces</i>)	Feces	Summer, AD 2015. Reservoir age estimate 70 ± 21 ¹⁴ C yr.	pMC 103.31 ± 0.26	-30.16	0.59	28.33	48.97	1.69
22231	Stanovoye 4, Russia	Elk (<i>Alces alces</i>)	Antler mattock	566 ± 64 ¹⁴ C yr older than its wooden shaft KIA-35157.	9426 ± 43	-21.83	4.68	3.65	43.28	13.86
KIA-35157	Stanovoye 4, Russia	N/A	Wooden shaft of AAR-22231 (Hartz et al. 2010)		8860 ± 47					
22232	Stanovoye 4, Russia	Elk (<i>Alces alces</i>)	Antler socket	92 ± 64 ¹⁴ C yr older than its wooden shaft KIA-35153.	9597 ± 43	-20.39	4.61	3.23	36.92	13.33

Table 1 (Continued)

AAR	Site	Species	Material	Comments	¹⁴ C age (pMC)	δ ¹³ C (‰ VPDB)	δ ¹⁵ N (‰ AIR)	C:N ratio	C %	N %
KIA-35153	Stanovoye 4, Russia	N/A	Wooden shaft of AAR-22232 (Hartz et al. 2010)		9505 ± 47					
24832	Aldersro, Denmark	Elk (<i>Alces alces</i>)	Antler	FHM4096x4701	7825 ± 44	-24.94	9.90	8.24	19.07	2.70
24833	Aldersro, Denmark	Yew/juniper (<i>Taxus/ Juniperus</i>)	Twig	Same context as AAR-24832.	10869 ± 43	-23.97	N/A	N/A	N/A	N/A
21802	Friesack 27, Germany	Elk (<i>Alces alces</i>)	Bone	F27-01 from layer complex 1	9441 ± 41	-21.85	5.33	3.26	43.82	15.69
21804	Friesack 27, Germany	Roe deer (<i>Capreolus capreolus</i>)	Bone	F27-08 from layer complex 1	9623 ± 38	-21.52	6.38	3.23	42.72	15.43
21803	Friesack 27, Germany	Elk (<i>Alces alces</i>)	Bone	F27-06 from layer complex 2	9587 ± 39	-22.14	4.51	3.19	43.02	15.73
21805	Friesack 27, Germany	Wild boar (<i>Sus scrofa</i>)	Bone	F27-12 from layer complex 2	9419 ± 38	-21.95	5.80	3.27	42.35	15.12
22223	Beregovaya II, Russia	Elk (<i>Alces alces</i>)	Bone	Aa-Ur-1961/226 from layer 2	7045 ± 32	-18.79	4.46	3.21	41.52	15.06
22224	Beregovaya II, Russia	Elk (<i>Alces alces</i>)	Bone	Aa-Ur-1961/228 from layer 2	7372 ± 31	-20.27	3.39	3.18	41.29	15.16
22225	Beregovaya II, Russia	Elk (<i>Alces alces</i>)	Bone	Aa-Ur-1961/236 from layer 2	7141 ± 35	-20.95	4.39	3.17	42.04	15.47
22226	Beregovaya II, Russia	Reindeer (<i>Rangifer tarandus</i>)	Bone	Aa-Ur-1961/247 from layer 2	7265 ± 34	-20.3	4.07	3.17	39.41	14.49

22227	Beregovaya II, Russia	Reindeer (<i>Rangifer tarandus</i>)	Bone	Aa-Ur-1961/640 from layer 2	7099 ± 32	-21.24	5.56	3.20	41.99	15.32
21801	Em, Denmark	Elk (<i>Alces alces</i>)	Antler	Antler 1948/69B. Attached to AAR-21800.	8608 ± 89	-21.49	3.12	3.29	43.46	15.42
21800	Em, Denmark	Elk (<i>Alces alces</i>)	Bone	Skull bone 1948/69B. Attached to AAR-21801.	8664 ± 41	-22.37	4.05	3.31	41.55	14.65
	Schauinsland, Germany			Atmosphere, growing season of 2015 (Levin et al. 2013 and pers. comm. Levin 2015)	pMC 104.22 ± 0.10					

IntCal13 (Table 1). The measured ages all agree within 2–3 σ with IntCal13. A reservoir effect can thus not be found here, although the individuals originate from an area with calcareous lakes, where freshwater reservoir effects can be expected. A sample of water plant from Melhus, probably *Potamogeton natans*, was collected in May 2015. Its pMC of 101.41 ± 0.41 is lower than the contemporaneous atmosphere (pMC = 104.21 ± 0.10 for the 2015 growing season, Table 1) and yields an estimated reservoir age of $R = 219 \pm 32$ ^{14}C yr (Eq. 1).

$$R = 8033 * \ln(\text{pMC}_{\text{atm}}/\text{pMC}_{\text{sample}}) \quad (1)$$

This indicates the possibility of a measurable reservoir effect, in case the elk consumed large amounts of plants with this radiocarbon age. In Figure 2, the calibrated radiocarbon ages of the historical elk from Norway are shown together with several simulated radiocarbon ages of samples with the same time of death. In the cases of the samples from Selbu and Melhus, both agree. However, in the case of the sample from Bratsberg, the measured and simulated radiocarbon ages agree better when assuming a reservoir age of about 100 ^{14}C yr for the elk.

Elk feces, collected in summer 2015 in Siberia, have a pMC of 103.31 ± 0.26 (Table 1). Compared to the average atmospheric pMC of the 2015 growing season, this results in a reservoir age estimate of 70 ± 21 ^{14}C yr (cf. Eq. 1). The shape and consistency of the feces pellet is uncharacteristic for summer feces of elk—these are reported as being soft and poorly formed due to the high nutrient and water content of summer browse compared to winter browse (Schwartz and Renecker 1998). The general appearance of the sample and its low ^{14}C reservoir age both indicate a diet high in woody plant parts, i.e. terrestrial plants. This is in contrast to the observed preference of Russian elk for aquatic habitats and diet in summer (Heptner et al. 1966; Heptner and Nasimovich 1967). It is difficult to interpret the (remarkably low) $\delta^{13}\text{C}$ value of the feces sample of -30‰ , as the isotopic baseline of the region is unknown. The $\delta^{15}\text{N}$ value of this sample is only 0.59 ‰ . ^{15}N -isotopic enrichment of feces relative to diet have been reported to be between 1.4 and 2.0 ‰ (Kielland 2001). Therefore, this individual's diet would have had an average $\delta^{15}\text{N}$ value of -0.8 to -1.4‰ , not unusual for stems and leaves of trees such as willows, birch and aspen (Kielland 2001).

At Stanovoye, the elk antler artifact is in one case 566 ± 64 ^{14}C yr older than its wooden handle, in the other case only 92 ± 64 (Table 1, Figure 3). This could indicate that one of the elk antler tools was affected by the freshwater reservoir effect. However, the possibility of reused old antler for making the tool cannot be excluded.

The elk antler sample from Aldersro is younger than the twig that was found associated with it (Table 1). This indicates that the twig had been redeposited. The twig was identified to yew or juniper. If the first is true, this sample is quite old for yew, as yew is reported to reappear after the ice age around 7800–7200 cal BP in Central Europe, or in the Late Atlantic and Subboreal in Northwestern Europe, and thus possibly much later than 10000 cal BC in Denmark (Deforce and Bastiaens 2007; Hageneder 2013).

Two pairs of samples from Friesack 27 were radiocarbon dated. In the sample pair from layer complex 1, the elk is younger than the roe deer; in the sample pair from layer complex 2, the elk is older than the wild boar (Table 1, Figure 3). This indicates that the layer complexes are not, as previously assumed, closed stratigraphic units, and that the bones can have been redeposited. Therefore, I cannot make a statement about a reservoir effect in the elk from this site.

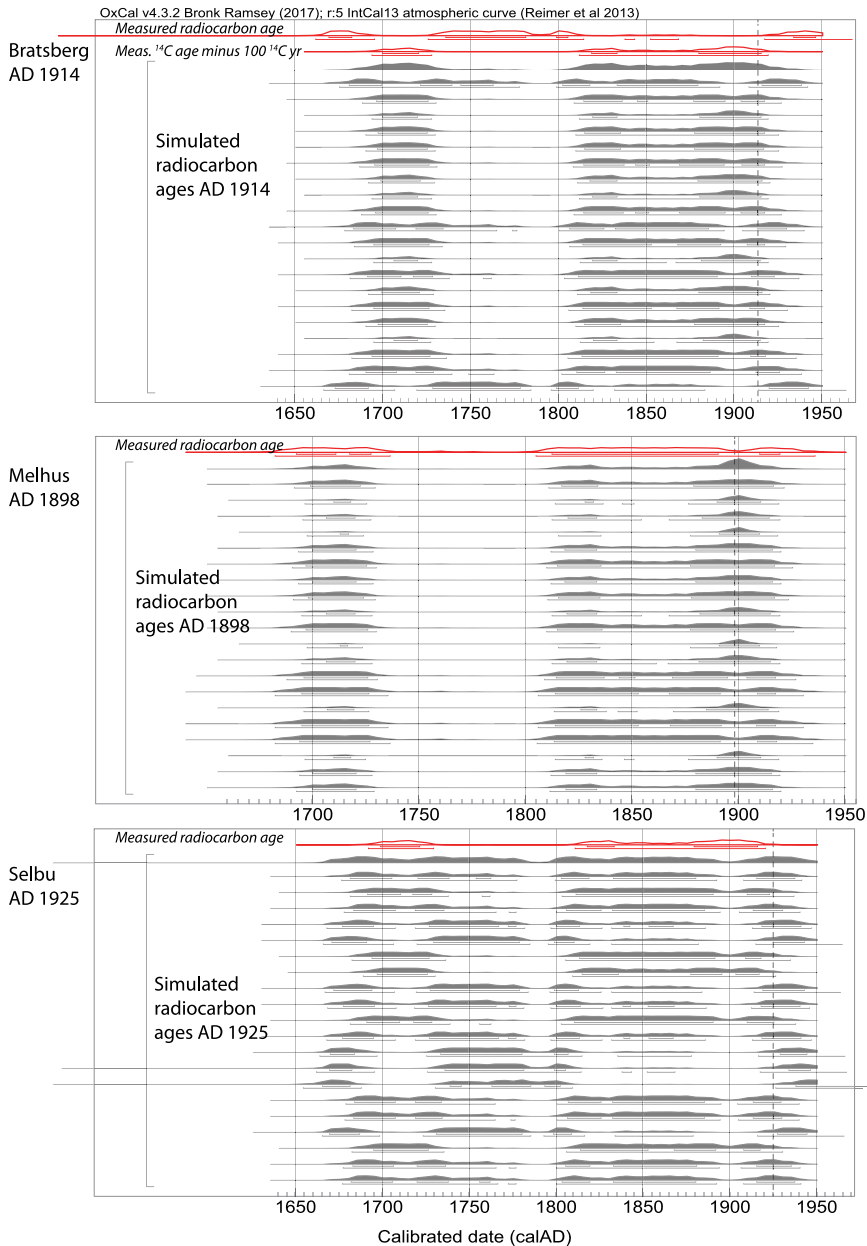


Figure 2 Calibrated and simulated radiocarbon ages of three historical elk samples from three sites in Norway (see Figure 1). Each panel represents one individual elk and site: the top panel the individual from Bratsberg, which died in AD 1914, the middle panel the individual from Melhus, which died in AD 1898, and the bottom panel the individual from Selbu, which died in AD 1925. Within each panel, the top probability distribution indicates the measured and calibrated radiocarbon age of the sample, shown in red outline (color figure available online). This is followed by 20 simulated radiocarbon ages for the time of death of the animal. A dashed line marks the time of death. In the case of Bratsberg, assuming a reservoir age of approximately 100 years results in a better match of the measured and simulated ages—the measured radiocarbon age minus 100 ^{14}C yr was calibrated as well and is shown as the second probability distribution, also in red outline. The samples were calibrated with OxCal 4.2.4 (Bronk Ramsey 2009; Ramsey and Lee 2013) and the terrestrial calibration curve IntCal13 (Reimer et al. 2013).

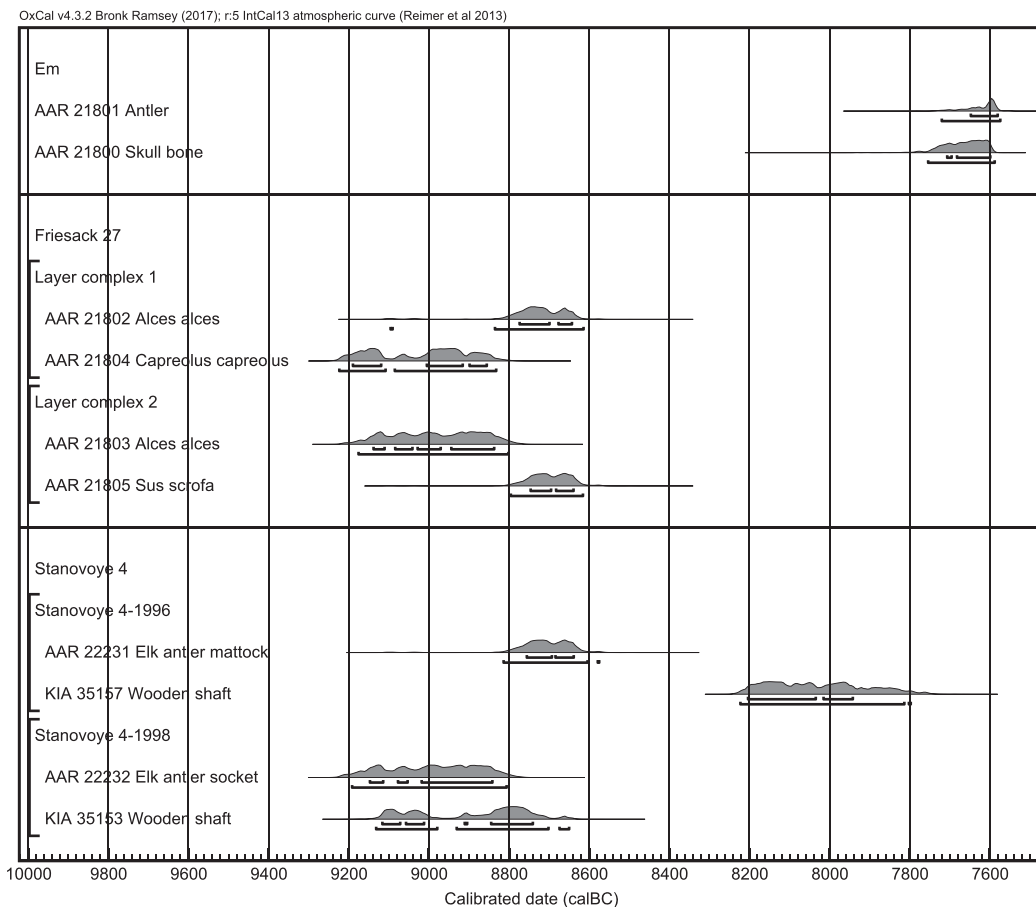


Figure 3 Calibrated radiocarbon ages of samples from Em (Denmark), Friesack 27 (Germany), and Stanovoye 4 (Russia; see Figure 1). The antler and skull bone from Em were still attached to another when found. Two pairs of samples from Friesack 27 originate from the same layer complexes and are thus assumed to be contemporaneous. From Stanovoye 4, two elk antler artifacts were dated, whose wooden handles had already been radiocarbon dated. The samples were calibrated with OxCal 4.2.4 (Bronk Ramsey 2009; Ramsey and Lee 2013) and the terrestrial calibration curve IntCal13 (Reimer et al. 2013).

A similar situation to that in Friesack can be found at Beregovaya II. From that site, I only dated samples belonging to layer 2. Unfortunately, those samples span a range of several hundred years, without any difference between elk and reindeer bones (Table 1, Figure 4). Previous food crust dates from this layer (Zhilin et al. 2014) fall into the same range.

The skull and antler samples from Em have approximately the same radiocarbon age. This illustrates that the carbon incorporated during summer in the antler is not affected by a greater reservoir effect than the year-round diet. However, this sample pair cannot be used to support nor to reject the possibility of a reservoir effect.

DISCUSSION

On the basis of the 20 samples analyzed in this study, I found age offsets between zero and over 500 years between the elk and associated samples. However, significant reservoir effects were

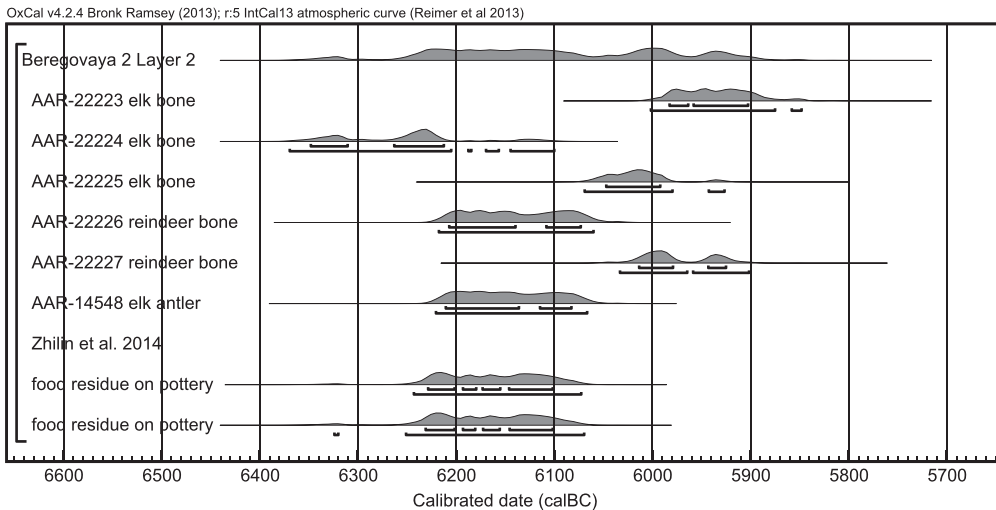


Figure 4 Calibrated radiocarbon ages of samples from Beregovaya II, layer 2, Russia. The samples were calibrated with OxCal 4.2.4 (Bronk Ramsey 2009; Ramsey and Lee 2013) and the terrestrial calibration curve IntCal13 (Reimer et al. 2013). They originate from the same layer and are assumed to be contemporaneous.

only found in few individuals and could also be explained by other factors, such as reuse of old antlers for tool production.

In all cases where elk samples were dated together with associated terrestrial samples from the same layers, I found discrepancies that cannot be caused by reservoir effects. For example, elk bones were both younger and older than the certainly terrestrial samples. In other cases, the terrestrial control samples also span a large age range. Individual layers do thus not represent closed contexts containing material of the same age. Even if the depositional event is considered to be of short duration, the sediment layers can contain redeposited material of different ages. For further studies regarding reservoir effects, I will thus aim at obtaining samples with better age controls than only the stratigraphic position.

The examples from Norway and Stanovoye 4 show that elks from the same region can have different reservoir ages. Therefore, the possibility of a reservoir effect in elk does not only depend on the study region (e.g., the presence of lakes with a considerable reservoir age), but also on the behavior of the individual elk. It should be noted that I only analyzed samples from Europe so far. From North America (Canada and the USA), there are numerous accounts of elk consuming large amounts of aquatic vegetation. In Ontario, for example, elk feed on aquatic vegetation from May/June to October, create access trails to feeding sites in lakes, and gather in groups of up to 20 individuals for feeding in one lake (Timmermann and Racey 1989). This could reflect the dietary preferences of elk in North America, or an observation bias, as elk are much easier to observe in and next to water than in a dense forest (Lenarz et al. 2011).

Several quantitative studies of elk nutrition found that aquatic plants only played a minor role. For example, the analysis of rumen contents of elk from Canada found only 4% aquatic plants in the elks' summer diet, while they were totally absent in the rumen contents of Alaskan elks (Cushwa and Coady 1976; Crête and Jordan 1981). When recording the species and bite size of every individual bite in elks' feeding bouts, LeResche and Davis (1973) found that 3% of the

plants consumed in summer were aquatic. The same method was applied to elks in a mountainous area of Alaska, where virtually no aquatic plants were consumed, probably due to the lack of aquatic habitat types in the study area (Van Ballenberghe et al. 1989). Only a few percent of radio locations of elks from Minnesota were in marsh habitat, although the elks were often observed to feed on aquatic vegetation from drainage ditches (Phillips et al. 1973). Incremental sampling of elk hooves for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses showed less seasonal variation than would be expected from the large isotopic differences between aquatic and terrestrial browse (LaZerte and Szalados 1982), leading to the conclusion that aquatic plants only constitute a minor portion of the summer diet (Kielland 2001). Blood samples of elk showed no $\delta^{15}\text{N}$ differences between summer and winter diet, but an enrichment of 0.5–0.6‰ was observed for the $\delta^{13}\text{C}$ values in winter, probably due to isotopic differences between foliage and shrub stems (Ben-David et al. 2001). Thus, aquatic resources appear to be less important in elk diet than previously assumed. Even the use of aquatic habitats for cooling in summer might be less pronounced than generally reported. For example, Lenarz et al. (2011) found that shade in dense vegetation was preferred to aquatic sites for cooling. As mentioned above, this discrepancy between expected and measured use of aquatic resources could be due to an observation bias.

In the one case studied here, I could not detect a difference between the radiocarbon ages of the antler and bone. In terms of radiocarbon age, thus, there was no significant difference between summer diet and whole-year diet in this individual. This agrees with measurements performed along the hairs of North American elk, where seasonal differences also were absent (Drucker et al. 2010).

I could not find a correlation between the elks' reservoir age and the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values of the bone collagen. This is probably due to the small proportion of aquatic diet and/or small isotopic differences between terrestrial and aquatic vegetation. Therefore, I do not have a tool to predict, let alone quantify, reservoir ages in elk.

The isotope values of my elk samples fall generally within the range of values measured on elk hair from boreal forests in Canada ($\delta^{13}\text{C}$ between -26 and -22 ‰, $\delta^{15}\text{N}$ between 0 and 7‰ for individual samples, Drucker et al. [2010]) and elk hooves from Alaska ($\delta^{13}\text{C}$ between ca. -24.5 and -22.5 ‰, $\delta^{15}\text{N}$ between ca. 1 ‰ and 2.5‰, Kielland [2001]), although my $\delta^{13}\text{C}$ values tend to be less negative. In this study by Drucker et al. (2010), however, there was a significant difference between the average values of elk hairs compared to caribou (reindeer) hair—the latter had consistently higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that did not overlap with those of the elk. This difference was interpreted as reflecting differences in diet between the two species. Therefore, the overlapping isotope values of my elk and reindeer samples from Beregovaya could indicate overlapping dietary resources and a general difference in habitats between prehistoric Russia and today's North America.

In the literature, there are very few cases of radiocarbon dated elk remains in well-dated contexts. For example, two Swedish elk samples were 500–1000 years older than the pollen-dated context—but the same applied to some truly terrestrial animals, so this probably indicates a problem with the pollen dating rather than a reservoir effect in the elk. A better example is the elk found at Miesenheim, Germany. Its age is well-constrained as it was found below the Laacher See tephra. This individual has been dated multiple times in the context of an intercomparison study, without an indication of reservoir effects (Kuzmin et al. 2018). Another example is from England, where at Poulton-le Fylde, a complete elk

skeleton with two bone or antler barbed points close to its hind bones was excavated in the 1970s (Barnes et al. 1971; Hallam et al. 1973). Both the skeleton, preservatives extracted from it and two samples of the surrounding detritus mud were radiocarbon dated (Hallam et al. 1973; Gillespie et al. 1985; Jacobi 1986). Amino acids extracted from elk bone have the same radiocarbon age as the older mud sample. However, in case the younger mud sample represented the “true age” of the event, this individual would have a reservoir age of about 700 ¹⁴C yr. For future studies, it would be advisable to date the barbed points found at the animal as well.

From Denmark, there are several examples of elk skeletons found in associations with hunting weapons made of bone or antler. These would serve as excellent test material to detect possible reservoir effects, unless of course all weapons had been made of elk bone or antler. At Skottemarke, Denmark, an elk skeleton was dated to 9400 ± 140 BP (K-2075). The author had also applied for radiocarbon dates of samples of the surrounding layers, but had been rejected (Sørensen 1978). The elk from another Danish site, Tåderup, had been found together with a bone point and later a harpoon (Ødum 1920). It is dated to 7810 ± 120 BP (K-2227, Sørensen 1978). The bone point and harpoon have not been dated yet.

CONCLUSIONS

Most elk remains appear to be free of reservoir effects. Further studies are needed to determine whether this is true in general or only an effect of the small number of samples analyzed here. The importance of aquatic plants in the diet of elk might be considerably lower than usually reported. Therefore, I propose that radiocarbon dating of contemporary elk samples could be a useful tool to monitor the contribution of aquatic vegetation to elk diet. Aquatic and terrestrial vegetation differ in concentrations of macronutrients (lipids, proteins, carbohydrates), which are usually routed to different tissues in the animal's body. Therefore, I suggest to analyze different tissues and different compounds from one tissue (e.g., amino acids from bone collagen) to reconstruct the elk's diet in detail.

This study shows that a freshwater reservoir effect can occur in individual samples. Radiocarbon dates of elk remains should thus be treated with caution.

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