Neolithisation through bone: Stable isotope analysis of human and faunal remains from Syltholm II, Lolland, Denmark

Kurt J. Gron [a], Darren R. Gröcke [b], Daniel Groß [c], Peter Rowley-Conwy [a], Harry K. Robson [a,d,*], Janet Montgomery [a]

[a] Department of Archaeology, Durham University, South Road, Durham DH1 3LE, the United Kingdom of Great Britain and Northern Ireland
[b] Department of Earth Sciences, Durham University, South Road, Durham DH1 3LE, the United Kingdom of Great Britain and Northern Ireland
[c] Museum Lolland-Falster, 4800 Nykøbing Falster, Denmark
[d] BioArCh, Department of Archaeology, University of York, York YO10 5DD, the United Kingdom of Great Britain and Northern Ireland

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ABSTRACT

Despite an increasing number of studies, the application of stable sulfur (δ^{34}S) isotope analysis to prehistoric bone collagen remains in its infancy. Conventionally, stable sulfur isotope compositions reflect coastal proximity and the interaction between humans and animals. Here, we undertook stable carbon (δ^{13}C), nitrogen (δ^{15}N) and sulfur (δ^{34}S) isotope analysis of human and faunal bone collagen. To understand the local environmental conditions as well as the husbandry regime employed by the first farmers, and investigate where the animals were raised or hunted in non-specific terms, we sampled 50 faunal, including wild and domestic taxa, and human remains from the Late Mesolithic to Early-Middle Neolithic (c. 4860–2310 cal BC) site of Syltholm II on the island of Lolland, Denmark. We show that the wild animals were obtained from multiple locations surrounding the prehistoric Syltholm Fjord, including forested and open landscapes, areas impacted by sea spray and saltmarshes. In contrast, the domestic taxa, especially cattle, were tightly managed for the majority of their lives based on their δ^{13}C and δ^{15}N isotope compositions, though were likely raised in multiple locations, including sea spray-affected areas, saltmarshes and wetlands, based on their δ^{34}S values. The domestic dogs had a broad range of δ^{13}C, δ^{15}N and δ^{34}S values, reflecting the consumption of varying degrees of marine foodstuffs, including animals that were sulfide-derived. Overall, our results contribute to a growing body of evidence for possible cultural and animal husbandry duality during the earliest Neolithic in southern Scandinavia.

1. Introduction

The theoretical discourse regarding the introduction of agriculture in southern Scandinavia has turned a corner. Nowhere could this be more obvious than in the recently published volume "Changing Identity in a Changing World", resulting from a conference hosted by Museum Lolland-Falster, Denmark, in June 2022 (Groß and Rothstein, 2023). There has been a recent sea change in our understanding, driven by model-building regarding how agriculture comes to the southern Scandinavian landscape (Gron and Sørensen, 2018), and in light of recent genetic evidence (Allentoft et al., 2024; Jensen et al., 2019). The key developments are: firstly, that the transition to agriculture in southern Scandinavia must be seen as a process lasting several hundred years. This is due to contradictory cultural and economic archaeological

evidence of continuity and change in the period from c. 4000–3700 cal BC (see Gron and Sørensen, 2018; Groß and Rothstein, 2023). Secondly, we now know that individuals with hunter-gatherer ancestry were still in the landscape during this period. Owing to a lack of evidence for genetic admixture with incoming farmers, the coexistence of Late Mesolithic (Ertebølle culture, c. 5400–4000 cal BC) and Early Neolithic (Funnel Beaker culture, c. 3900–2600 cal BC) populations seems highly likely in some areas (Jensen and Sørensen, 2023; Jensen et al., 2019). Indeed, this coexistence may have included socio-cultural constraints on genetic exchange, such as taboos (see Gron and Sørensen, 2018; Groß and Rothstein, 2023).

Traditionally, Early Neolithic (EN) sites were separated into two categories: catching and settlement sites (Johansen, 2006). Catching sites are defined as being dominated by wild species and settlement sites

by domestic. With the blurring of the lines regarding the process of Neolithisation the meaning of this dichotomy has shifted somewhat. The key question is now whether actual farming is occurring at the site, near to it, or not at all (Gron, 2020; Gron and Sørensen, 2018). This is because the simple presence of domesticated animals cannot necessarily be taken to indicate active local husbandry (Gron, 2023). Indigenous populations can obtain domestic taxa and their products (e.g. dairy fats, such as milk, yoghurts, cheese and butter) through various means without doing any farming themselves (Gron, 2023; Lucquin et al., 2023). On the same note, this raises the question: what criteria are applied when defining a site as "Neolithic"? Is it a purely chronological argument or should mode (s) of subsistence play a relevant role in this classification?

To a certain extent, this then means that *when* a site was occupied in the period between the Late Mesolithic and the Early Neolithic matters less than *by whom*. The faunal assemblage from Syltholm II (MLF00906), Lolland, Denmark, falls directly into the middle of this area of uncertainty, because it contains a mixture of wild and domestic taxa and has been dated to span the transition to agriculture (c. 4660–2470 cal BC). However, the dating of the site is complex as it represents an accumulation over a longer period (i.e. a palimpsest) within the riparian zone of the former Syltholm Fjord. Stratigraphy at the site is complicated – it is partly reworked, and incorporates several phases of high-energy events, including storms and floods, as well as still-water episodes, representing lagoonal conditions during use of the site. Noteworthy finds from Syltholm II include a large number of organic artefacts, including stakes and tools (e.g. a shafted axe, paddles and spears), which were deliberately driven into the former seabed. Indeed, one feature, "Structure A", at the site has received considerable attention. It is considered a depositional/ritual space and one where mandibles of different taxa were deposited over the course of c. 800 years, spanning the Mesolithic-Neolithic transition (see Sørensen, 2020).

While the majority of the fauna from the site can be said to date to the period in question, the only way to know for sure is to directly AMS radiocarbon date each individual specimen ($n > 8200$), which is simply not practicable. Note also, that from the site Syltholm II, subunit III (MLF00906-III), only c. 10 % of the total faunal assemblage ($n = 3032$) has been species determined; subunit refers to a subdivision of the site and was implemented during the excavations, it is comparable to a trench number. Further information regarding the site and its background can be found in Jensen and Sørensen (2023), Måge et al. (2023), and Sørensen (2023).

The faunal assemblage (Table 1) from Syltholm II (Fig. 1) has the potential to be central to addressing the following: how the transition from the Mesolithic to the Neolithic might have taken place and in what way new species were introduced in different social settings. Presently, the assemblage contains roughly 7 % domestic taxa or *c.* 21 % if indetermined specimens, insects and others, are excluded. This figure also includes domestic dogs that make up *c.* 3 % of the assemblage but excludes undifferentiated swine, which comprise a similar proportion. To understand the role of animals at the site and their exploitation by humans across the transition to agriculture, we aim to address the following questions: did the domestic and wild taxa live in the same or different environments? Did they feed differently? How did they feed? Are there inter-species differences? All of these questions may provide insight into the economy and activities at Syltholm II and clarify its place in the Neolithisation process.

Fig. 1. Location of Syltholm II (base-map by Vemaps, https://vemaps.com /denmark/dk-05).

To investigate these questions, we undertook stable carbon (δ^{13}C), nitrogen (δ^{15}N) and sulfur (δ^{34}S) isotope analysis of bone collagen. Our aim was to understand the local environmental conditions as well as the husbandry regime employed with regards to the domestic taxa. We further aimed to investigate where animals were raised or hunted in non-specific terms. Ultimately, we present evidence of landscape use during the transition to agriculture on the island of Lolland and if, and how, domesticated taxa were incorporated into the previous wild-animal based economy.

2. Materials and methods

Fifty bone samples were selected for stable isotope analysis from the site of Syltholm II, subunit III (MLF00906-III). These include individuals attributed to domestic cattle (*Bos taurus*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), red fox (*Vulpes vulpes*), ovicaprids (*Capra* sp./ *Ovis* sp.), domestic dog (*Canis familiaris*), humans (*Homo sapiens*) and sheep (*Ovis aries*). Sample information and data are shown in Table 2. Minimum Number of Individuals (MNI) data were not available for the assemblage, so an attempt was made to select the same skeletal element from a given taxon, and from the same side of the body where possible. MNI values were then established through side-by-side comparison using a manual overlap method supplemented by gross differences in size, age, etc. Consequently, a minimum of three cattle, two-ovicaprids, one fox, six dogs, one human, three red deer, and four roe deer are present within the sample set. To buffer against the chances of insufficient collagen preservation a greater number of specimens were selected

Table 1

Summary of the number of specimens of the different animal groups from the Syltholm II sites. Note that MLF00906-III has not yet been fully analysed. The category "other" includes small rodents, amphibians, and fossils.

Sub-site	Domestic mammals	Wild terrestrial mammals	Marine mammals	Birds	Fish	Insects	Other	Unidentified	Total
MLF00906-I	409	357		49	144	7	2	1816	**2784**
MLF00906-II	123	255	3	130	1182	11	33	669	**2406**
MLF00906-III	80	100	8	17	79	4		2744	**3032**
Total	**612**	**712**	**11**	**196**	**1405**	**22**	**35**	**5229**	**8222**

Table 2
Sample information and obtained stable carbon, nitrogen and sulfur isotope compositions from Syltholm II (MLF00906-III). Key: struck through – unacceptable data (see text).

Find No.	Taxon	Element	Side	SIBL ID	Collagen yield (%)	%C	δ¹³C (‰)	%N	δ¹⁵N (‰)	%S	δ³⁴S (‰)	C:N atomic	C:S atomic	N:S atomic	Comments
X1374	*Bos taurus*	Metacarpal	L	9348	13.54	38.54	−21.43	13.84	3.56	~~0.36~~	~~−4.15~~	3.25	~~286~~	~~88~~	Discarded S data
X4894	*Bos taurus*	Metacarpal	R	9359	16.64	44.61	−21.90	15.68	3.78	0.24	15.65	3.32	496	150	
X19316	*Bos taurus*	Mandible	R	9362	14.52	44.77	−21.08	16.06	3.75	0.19	6.97	3.25	629	194	
X14108	*Bos taurus*	Metacarpal	L	9365	9.87	38.87	−21.57	13.91	3.23	~~0.78~~	~~−13.82~~	3.26	~~133~~	~~41~~	Discarded S data
X8759	*Bos taurus*	Mandible	L	9373	10.90	39.81	−21.82	14.66	4.84	0.36	−4.64	3.17	295	93	
X8039	*Bos taurus*	Mandible	R	9378	12.18	41.66	−21.99	15.13	4.65	~~0.46~~	~~−11.42~~	3.21	~~242~~	~~75~~	Discarded S data
X1401	*Bos taurus*	Mandible	R	9384	11.12	42.15	−21.55	14.71	4.55	0.33	−5.33	3.34	341	102	
X14109	*Bos taurus*	Metacarpal	L	9388	11.75	37.60	−21.83	14.35	4.96	~~0.39~~	~~−10.16~~	3.05	~~257~~	~~84~~	Discarded S data
X3438	*Bos taurus*	Metacarpal		9380	8.97	42.86	−21.90	15.39	4.09	0.23	4.79	3.25	498	153	
X19704	*Canis familiaris*	Mandible	R	9382	11.55	39.13	−16.58	14.28	9.55	0.26	0.73	3.20	402	126	
X110	*Canis familiaris*	Radius	R	9358	19.07	45.28	−11.95	16.10	10.28	0.22	5.48	3.28	550	168	
X5094	*Canis familiaris*	Radius	R	9360	18.77	45.79	−12.45	15.98	10.37	0.22	12.75	3.34	556	166	
X19980	*Canis familiaris*	Mandible	R	9367	13.79	44.37	−10.66	15.44	12.28	~~0.42~~	~~3.67~~	3.35	~~282~~	~~84~~	Discarded S data
X2101	*Canis familiaris*	Radius	R	9370	16.22	40.04	−15.00	14.87	9.77	0.33	−3.22	3.14	324	103	
X18439	*Canis familiaris*	Radius	R	9375	19.11	39.39	−10.29	14.82	9.96	0.22	10.91	3.10	478	154	
X1036	*Canis familiaris*	Radius	R	9376	17.68	42.91	−13.17	15.74	10.79	0.27	2.57	3.18	424	134	
X19821	*Canis familiaris*	Mandible	R	9383	12.24	41.54	−13.76	14.75	10.18	0.31	−4.78	3.28	358	109	
X18168	*Canis familiaris*	Mandible	R	9385	13.87	40.20	−10.11	14.38	9.54	0.29	−2.73	3.26	370	114	
X1000	*Canis familiaris*	Mandible	R	9386	12.45	42.08	−13.87	15.07	10.38	0.28	−6.60	3.26	401	123	
X19756	*Canis familiaris*	Mandible	R	9389	8.42	47.55	−22.38	17.35	5.33			3.20			
X4950	*Capra* sp./*Ovis* sp.	Metacarpal		9342	11.43	43.34	−24.47	15.17	4.26	~~0.64~~	~~−11.51~~	3.33	~~181~~	~~54~~	Discarded S data
X1051	*Capra* sp./*Ovis* sp.	Metacarpal	R	9366	5.58	27.20	−22.44	9.54	2.81	~~0.69~~	~~−5.06~~	3.32	~~105~~	~~32~~	Discarded S data
X14902	*Capreolus capreolus*	Metacarpal		9343	19.18	43.21	−22.03	15.07	5.24	~~0.45~~	~~−0.74~~	3.35	~~256~~	~~77~~	Discarded S data
X4941	*Capreolus capreolus*	Scapula	R	9356	17.27	40.25	−23.91	15.33	4.83	0.27	8.02	3.06	398	130	
X3061	*Capreolus capreolus*	Metacarpal	R	9341	15.59	41.23	−22.57	14.78	4.10	0.27	11.31	3.25	408	125	
X16630	*Capreolus capreolus*	Metacarpal	L	9346	15.73	45.44	−20.91	15.57	5.28	~~0.42~~	~~2.54~~	3.40	~~289~~	~~85~~	Discarded S data
X9519	*Capreolus capreolus*	Scapula	R	9349	15.22	41.44	−22.04	14.39	4.53	0.33	4.87	3.36	335	100	
X7661	*Capreolus capreolus*	Scapula	R	9361	16.90	46.04	−22.15	16.51	4.49	0.25	7.92	3.25	492	151	
X18612	*Capreolus capreolus*	Metacarpal		9364	16.38	45.41	−21.69	16.00	5.00	0.23	10.64	3.31	527	159	
X18613	*Capreolus capreolus*	Metacarpal	L	9369	15.19	42.70	−22.02	15.09	5.49	0.28	10.71	3.30	407	123	
X19078	*Capreolus capreolus*	Metacarpal	R	9379	9.05	41.71	−23.24	15.21	5.10	0.27	−1.54	3.20	412	129	
X22545	*Capreolus capreolus*	Metacarpal	L	9381	13.57	44.93	−23.04	14.99	5.01	0.22	5.02	3.50	545	156	
X2524	*Cervus elaphus*	Calcaneus	L	9353	19.47	43.25	−23.10	16.14	6.47	0.25	14.57	3.12	462	148	
X20416	*Cervus elaphus*	Astragalus	R	9354	20.36	41.47	−22.56	16.10	5.11	0.28	12.81	3.00	395	132	
X14041	*Cervus elaphus*	Calcaneus	L	9340	10.30	40.73	−20.71	14.60	4.51	~~0.61~~	~~−10.24~~	3.25	~~178~~	~~55~~	Discarded S data
X20413	*Cervus elaphus*	Calcaneus	R	9344	16.33	44.17	−22.49	15.67	4.51	0.37	9.96	3.29	319	97	
~~X14046~~	~~*Cervus elaphus*~~	~~Astragalus~~	R	9347	8.94	~~6.08~~	~~−23.57~~	~~2.32~~	~~−0.93~~	~~2.10~~	~~−16.93~~	~~3.06~~	~~8~~	~~3~~	Discarded C, N and S data
X17488	*Cervus elaphus*	Astragalus	L	9350	18.81	45.61	−22.77	16.13	4.70	0.31	15.71	3.30	393	119	
X11317	*Cervus elaphus*	Calcaneus	R	9351	18.09	41.67	−22.70	14.89	4.75	0.30	8.31	3.26	371	114	
X16166	*Cervus elaphus*	Astragalus	R	9363	14.72	44.94	−22.72	15.87	5.20	0.16	8.91	3.30	750	227	
X19604	*Cervus elaphus*	Astragalus	L	9368	13.32	46.28	−21.86	16.71	4.46	0.24	15.68	3.23	515	159	
X5545	*Cervus elaphus*	Calcaneus		9372	16.06	38.18	−23.41	14.39	5.33	0.35	−5.77	3.09	291	94	
X8775	*Cervus elaphus*	Calcaneus	L	9390	3.55	43.46	−20.25	15.46	8.13			3.28			
~~X316~~	~~*Cervus elaphus*~~	~~Astragalus~~	L	9391	14.28	~~10.77~~	~~−23.55~~	~~2.87~~	~~3.04~~			4.38			Discarded C and N data
X14603	*Homo sapiens*	Cranium		9371	14.50	40.22	−20.90	14.57	8.83	~~0.44~~	~~−10.84~~	3.22	~~244~~	~~76~~	Discarded S data
X2338	*Homo sapiens*	Cranium		9377	5.97	37.61	−21.11	14.00	9.12	~~0.93~~	~~−16.26~~	3.13	~~108~~	~~34~~	Discarded S data
X14604	*Homo sapiens*	Cranium		9387	15.03	41.39	−20.82	14.71	8.70	0.37	−13.71	3.28	299	91	
X4196	*Ovis aries*	Femur	R	9374	14.03	43.59	−22.45	15.45	5.77	0.22	6.13	3.29	529	161	
X3845	*Vulpes vulpes*	Humerus	R	9345	14.43	43.57	−18.79	15.45	9.43	0.27	9.67	3.29	431	131	
X409	*Vulpes vulpes*	Metacarpal	L	9355	21.62	44.49	−13.18	15.76	9.57	0.28	9.82	3.29	424	129	

than individuals indicated by the overall MNI, additional individuals are almost certainly represented within this sample.

Preparation work was undertaken in the Isotope Laboratory in the Department of Archaeology at Durham University and subsequent analyses were performed in the Stable Isotope Biogeochemistry Laboratory (hereafter SIBL) in the Department of Earth Sciences at Durham University. Bone collagen was extracted and purified following standard preparation protocols that were based on a modified Longin (1971) method (Ambrose and DeNiro, 1986; DeNiro, 1985; O'Connell and Hedges, 1999). Briefly, the bone samples for collagen extraction were removed from larger skeletal elements using a diamond-tipped rotary dental saw and then cleaned of potential surface contamination using a tungsten-carbide rotary burr. The sherds (*c.* 160–1200 mg) were submerged in a 0.5 M HCl solution at 4 °C until demineralised. Once complete, the samples were rinsed in deionised water three times, and then placed in solution to pH3. The samples were heated at 70 °C for 48 h, and then the supernatant, including the collagen, was filtered using Polyethylene Ezee filters (Elkay Laboratories Ltd., Basingstoke, UK). Lastly, the samples were frozen at −20 °C, lyophilised, and weighed into tin capsules (~1.0–1.5 mg) for stable isotope analysis. In general, priority was given to the stable carbon and nitrogen isotope analysis.

Stable carbon and nitrogen isotope analysis of the human and faunal bone collagen samples was undertaken using an ECS 4010 elemental analyser (Costech, Valencia, CA, USA) connected to a Delta V Advantage isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany). Accuracy was monitored by the repeated analyses of in-house standards (e.g. glutamic acid, $\delta^{13}C$ = -11 ‰, $\delta^{15}N$ = -7.5 ‰; IVA urea, $\delta^{13}C$ = -43.26 ‰, $\delta^{15}N$ = -0.56 ‰; col-pure collagen, $\delta^{13}C$ = -17.9 ‰, $\delta^{15}N$ = 6.6 ‰; and spar calcite, $\delta^{13}C$ = 2.9 ‰), which were integrated into the run sequence. A range of international standards (e.g. USGS 40, USGS 24, IAEA-600, IAEA-CH-3, IAEA-CH-7, IAEA-N-1, IAEA-N-2) were similarly integrated and analysed. These standards yielded an analytical range of −46 ‰ to + 3 ‰ in $\delta^{13}C$, and −4.5 ‰ to + 20.4 ‰ in $\delta^{15}N$. The analytical uncertainty in $\delta^{13}C$ and $\delta^{15}N$ was < 0.2 ‰ for replicate analysis of the in-house standards and replicate analysis of the samples, and ± 0.1 ‰ for replicate analyses of the international standards. Total organic carbon and nitrogen was obtained as part of the stable isotope analysis using an in-house standard (glutamic acid, C = 40.82 %, N = 9.52 %).

Stable sulfur isotope analysis of the human and faunal bone collagen samples was undertaken using an EA IsoLink (Thermo Scientific, Bremen, Germany) connected to a Delta V Plus isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany). Accuracy was monitored by the repeated analysis of an in-house standard (e.g. sulfanilamide) as well as a range of international standards (e.g. IAEA-SO-5, IAEA-SO-6, NBS-127), which were integrated into the run sequence. These standards yielded an analytical range of −31 ‰ to + 20.3 ‰ in $\delta^{34}S$. The analytical uncertainty in $\delta^{34}S$ was < 0.3 ‰ for replicate analysis of the in-house standards and replicate analysis of the samples, and < 0.2 ‰ for replicate analyses of the international standards. Total organic sulfur was obtained as part of the stable isotope analysis using an in-house standard (sulfanilamide, S = 18.62 %).

3. Results

Of the 50 samples selected for stable isotope analysis, a total of 48 $\delta^{13}C$ and $\delta^{15}N$ values as well as 34 $\delta^{34}S$ values were obtained (Table 2). It is possible that the low sulfur success rate is the result of diagenetic contamination of the burial environment with sulfides. All data are plotted in Fig. 2. There were insufficient quantities of collagen to measure the stable sulfur isotope compositions in three samples as priority was given to the stable carbon and nitrogen isotope analysis. All atomic C:N ratios were within the acceptable range of 2.9–3.6 (DeNiro, 1985) with a single exception (Sample 9391), which is not considered further. A further specimen (Sample 9347) yielded very low carbon and nitrogen percentages and is also deemed unacceptable. Thirty-one of the atomic

C:S ratios and 30 of the atomic N:S ratios fell within the acceptable ranges for mammal bone collagen (i.e. 600 ± 300 and 200 ± 100 respectively) given by Nehlich and Richards (2009). However, stable sulfur isotope analysis of vanadium pentoxide (V_2O_5) from various suppliers has revealed a sulfur blank issue (Gröcke unpublished) and thus, SIBL employs tungsten oxide (WO_3) as a combustion additive to the collagen sample. In addition, sample collagen weights were much less (~1.5 mg) as SIBL uses an EA IsoLink (Thermo Scientific, Bremen, Germany), including a temperature ramped GC system, connected to a Delta V Plus isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany). Since previous studies use sample collagen weights in the order of 10 mg, which quickly absorbs considerable water that interferes and reduces the amount of SO_2 being produced in the system — this would under-estimate the amount of sulfur in a sample, thus increasing the atomic C:S and N:S ratios. Therefore, in this study we accept atomic C:S and N:S ratios that were 10 % higher or lower than the standard deviations of the acceptable ranges (i.e. 270–930 and 90–310 respectively) suggested by Nehlich and Richards (2009). This resulted in additional acceptable atomic C:S ratios (n = 3) and atomic N:S ratios (n = 4). Mean and standard deviations as well as maximum and minimum $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values are presented by taxon in Table 3, while the full dataset in provided in Table 2.

4. Discussion

4.1. $\delta^{13}C$ and $\delta^{15}N$ compositions

The herbivore (cattle, ovicaprids, roe deer, and red deer) $\delta^{13}C$ (-24.5 ‰ to −20.3 ‰) and $\delta^{15}N$ (2.8 to 8.1 ‰) values (Fig. 2A and 3) from Syltholm II (MLF00906-III) are similar to herbivorous taxa throughout the region (see Gron and Rowley-Conwy, 2017). One anomalously high (in both $\delta^{13}C$ and $\delta^{15}N$) red deer is present (Sample 9390), which could represent an individual that had not yet been weaned as the calcaneus was broken in such a way it was not possible to determine elemental fusion at its proximal end. It could also represent an individual feeding in a coastal environment, such as a saltmarsh (e.g. Guiry et al., 2021a). For example, a broad range of $\delta^{15}N$ values (range = 3.9 ‰ to 8.8 ‰; $\delta^{15}N_{mean}$ = 6.4 ‰; SD = 1.1; n = 80), were obtained from cattle and sheep bone collagen from 17th-18th C AD Acadian settlements in Canada. When their $\delta^{13}C$ and $\delta^{34}S$ values were also considered, the authors demonstrated that the herbivores had grazed in saltmarshes (Guiry et al., 2021a). Alternatively, the red deer may have consumed seaweed (e.g. Conradt, 2000). For instance, at Quanterness on the island of Orkney, UK, stable carbon and nitrogen isotope analysis of Middle-Late Neolithic juvenile sheep, between 0 and 3 months old, yielded similarly high $\delta^{15}N$ values between 7.5 ‰ and 9.6 ‰ ($\delta^{15}N_{mean}$ = 8.7 ‰; SD = 0.8; n = 6), which were interpreted as the result of seaweed consumption (Schulting et al., 2017).

No cattle have $\delta^{13}C$ values lower than c. –22 ‰ (Fig. 2A and 3), indicating that they were browsing in more open environments and were being tightly controlled in their grazing, again typical for Early Neolithic southern Scandinavian cattle (e.g. Gron and Rowley-Conwy, 2017; Noe-Nygaard et al., 2005). The ovicaprids did not have similar $\delta^{13}C$ values. Instead, they sourced a substantial proportion of their diets in or from forests as indicated by $\delta^{13}C$ values lower than c. –22 ‰, which were more similar to many of the deer (Fig. 2A and 3). This likely demonstrates that they were not managed.

The human $\delta^{13}C$ values indicate the consumption of predominantly terrestrial protein (see Fischer et al., 2007) and at a higher trophic position than the herbivores (Bocherens and Drucker, 2003), likely indicating a diet composed of meat and/or dairy products (Fig. 2A). Moreover, since the differences between the three samples ($\delta^{13}C$ = 0.3 ‰; $\delta^{15}N$ = 0.4 ‰) were lower than the thresholds reported by Fahy et al. (2017) and Hyland et al. (2022), it is possible that we are dealing with a single individual, which corresponds with the MNI determination. The dogs were also feeding at a similar trophic position as the humans as
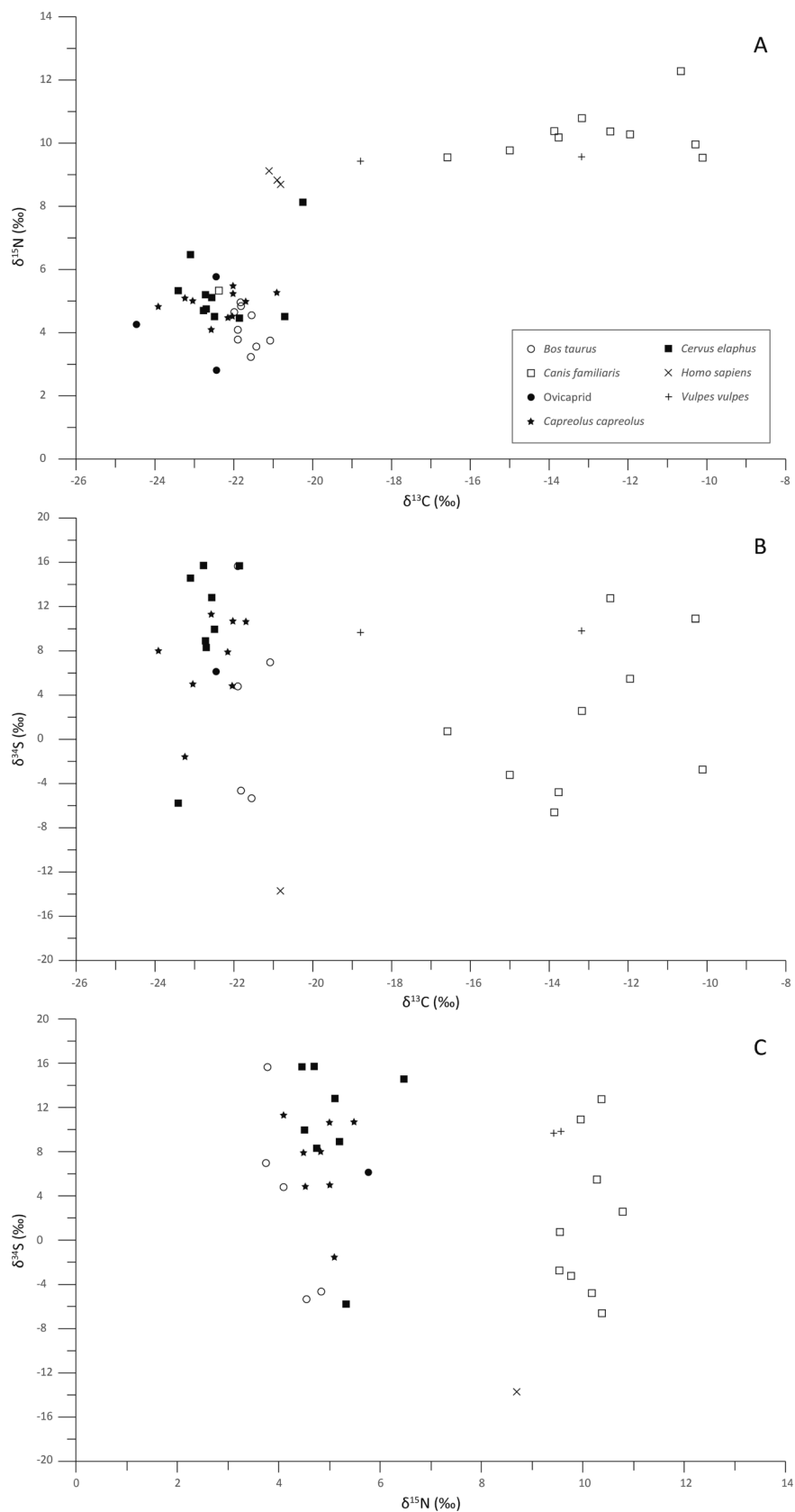
Fig. 2. Bone collagen isotopic compositions from Syltholm II (MLF00906-III). (A) Plot of $\delta^{13}C$ and $\delta^{15}N$ values. (B) Plot of $\delta^{13}C$ and $\delta^{34}S$ values. (C) Plot of $\delta^{15}N$ and $\delta^{34}S$ values.
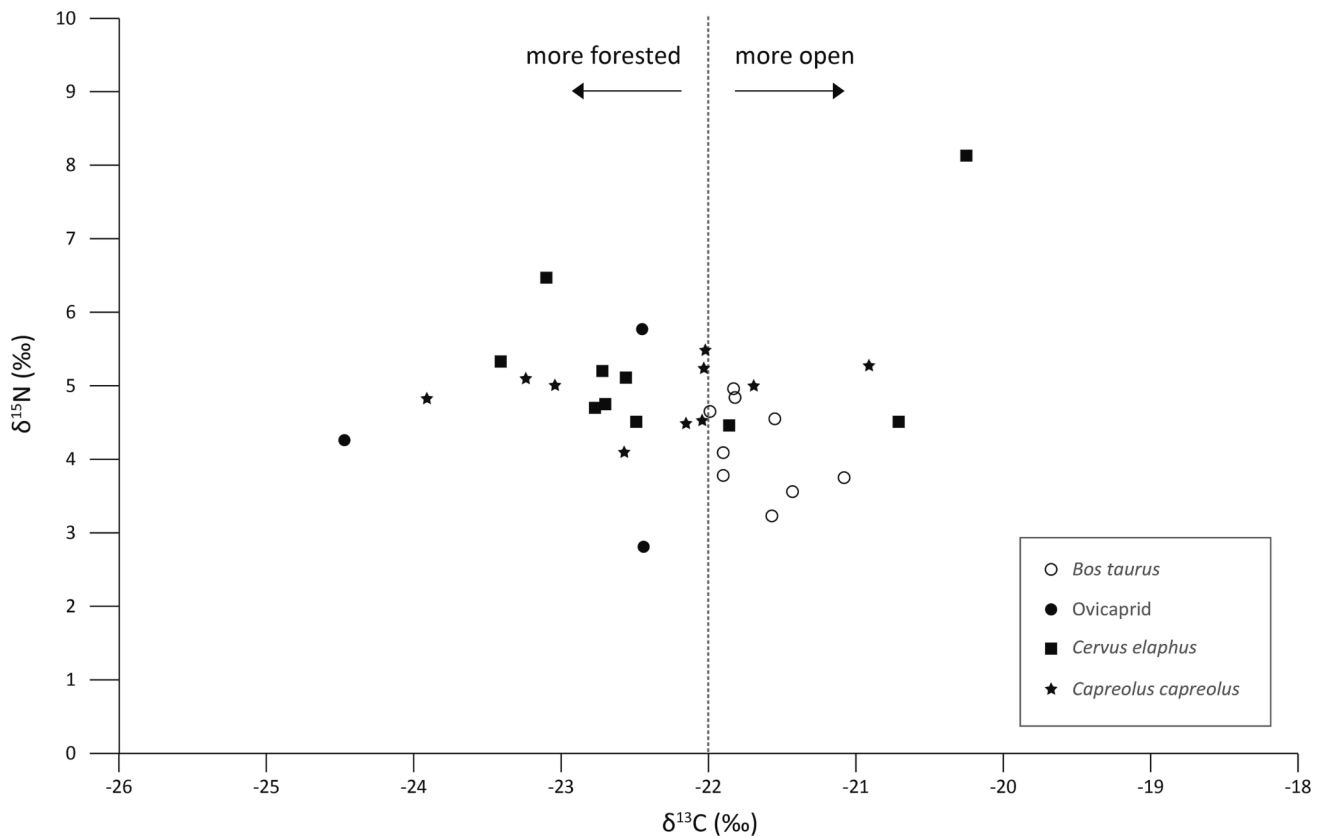
Fig. 3. Herbivore $\delta^{13}C$ and $\delta^{15}N$ values from Syltholm II (MLF00906-III).

Table 3
Summary statistics for the bone collagen isotopic compositions from Syltholm II (MLF00906-III).

Taxa	N	Mean ± SD $\delta^{13}C$ (‰)	Max $\delta^{13}C$ (‰)	Min $\delta^{13}C$ (‰)
Bos taurus	9	−21.68 ± 0.29	−21.08	−21.99
Canis familiaris	11	−13.66 ± 3.52	−10.11	−22.38
Ovicaprid	3	−23.12 ± 1.17	−22.44	−24.47
Capreolus capreolus	10	−22.36 ± 0.86	−20.91	−23.91
Cervus elaphus	10	−22.26 ± 1.02	−20.25	−23.41
Homo sapiens	3	−20.94 ± 0.15	−20.82	−21.11
Vulpes vulpes	2	−15.98 ± 3.97	−13.18	−18.79
Taxa	**N**	**Mean ± SD $\delta^{15}N$ (‰)**	**Max $\delta^{15}N$(‰)**	**Min $\delta^{15}N$(‰)**
Bos taurus	9	4.16 ± 0.62	4.96	3.23
Canis familiaris	11	9.86 ± 1.68	12.28	5.33
Ovicaprid	3	4.28 ± 1.48	5.77	2.81
Capreolus capreolus	10	4.91 ± 0.42	5.49	4.10
Cervus elaphus	10	5.32 ± 1.15	8.13	4.46
Homo sapiens	3	8.88 ± 0.21	9.12	8.70
Vulpes vulpes	2	9.5 ± 0.10	9.57	9.43
Taxa	**N**	**Mean ± SD $\delta^{34}S$ (‰)**	**Max $\delta^{34}S$ (‰)**	**Min $\delta^{34}S$ (‰)**
Bos taurus	5	3.49 ± 8.74	15.65	−5.33
Canis familiaris	9	1.68 ± 6.87	12.75	−6.60
Ovicaprid	1	6.13		
Capreolus capreolus	8	7.12 ± 4.29	11.31	−1.54
Cervus elaphus	8	10.02 ± 7.03	15.71	−5.77
Homo sapiens	1	−13.71		
Vulpes vulpes	2	9.75 ± 0.11	9.82	9.67

demonstrated by their higher $\delta^{15}N$ values relative to the herbivores. In terms of the proportion of marine protein in the dog diets, there is substantial inter-individual variability as demonstrated by their $\delta^{13}C$ values. Although freshwater resources can exhibit a wide range of $\delta^{13}C$ compositions (see Guiry, 2019), the archaeological context strongly implies the contribution of marine resources to diet. Notably, three individuals (Samples 9385, 9375 and 9367) have $\delta^{13}C$ values of −10.1 ‰, −10.3 ‰ and −10.7 ‰, corresponding to a marine diet. In contrast, there were two individuals (Samples 9370 and 9382) with intermediary $\delta^{13}C$ values of −15.0 ‰ and −16.6 ‰, demonstrating that a mixture of foodstuffs, including some marine foods, had been consumed. A further individual (Sample 9389) has a $\delta^{13}C$ value of –22.4 ‰, corresponding to a terrestrial diet (Fig. 2A; see Fischer et al., 2007). The two fox specimens have $\delta^{15}N$ values similar to those of the dogs (Fig. 2A), reflecting the consumption of high-protein foods. Similarly, their $\delta^{13}C$ values of −18.8 ‰ (Sample 9345) and −13.2 ‰ (Sample 9355) (Fig. 2A), represent an individual that consumed similar foodstuffs to the humans, and one that ate an appreciable amount of marine resources, perhaps inclusive of birds and eggs as has been demonstrated elsewhere (see Carbonell Ellgutter et al., 2020).

While there is a clear separation between the domestic dogs and the herbivores in both $\delta^{13}C$ and $\delta^{15}N$, there is considerable overlap among the herbivores (Fig. 4). Most notably is the similar range of $\delta^{13}C$ values among the wild deer and the more restricted range in $\delta^{13}C$ values among the cattle. The domestic dogs have higher $\delta^{15}N$ values than the herbivores, which is typical of a carnivore's placement within the trophic spectrum (e.g. Bocherens and Drucker, 2003). Among the herbivores, the red deer have the largest range of $\delta^{15}N$ values, the roe deer the most restricted, and the cattle intermediate. These differences may reflect the breadth of an individual taxon's dietary niche, the local environment, or other factors such as the locality from which the individual in question was hunted. The cattle also have slightly lower $\delta^{15}N$ values than the other herbivores, which is probably indicative of their feeding in more

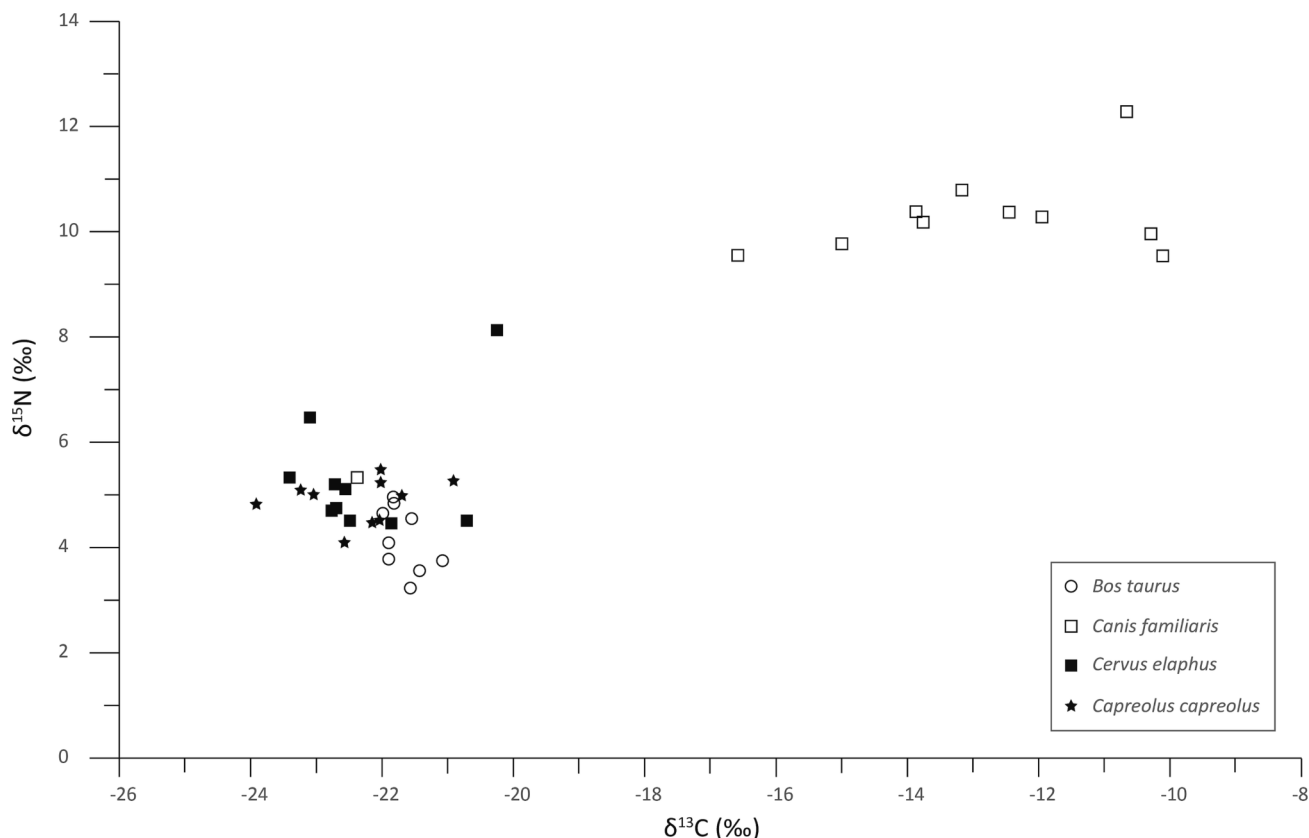**Fig. 4.** $\delta^{13}C$ and $\delta^{15}N$ values for taxa with more than three samples (see also Fig. 2A).

open environments with higher $\delta^{13}C$ values, environments which typically have lower $\delta^{15}N$ values than those that are more closed (Drucker et al., 2003).

4.2. $\delta^{34}S$ compositions

Stable sulfur ($\delta^{34}S$) isotope compositions from bone collagen reflect a number of factors, including diet, coastal proximity, and geology (Nehlich, 2015). As such, $\delta^{34}S$ ratios are commonly measured to complement stable $\delta^{13}C$ and $\delta^{15}N$ isotope analysis. A substantial range of $\delta^{34}S$ values were obtained from the human and faunal remains from Syltholm II (MLF00906-III): from -13.7 ‰ to $+15.7$ ‰ (Fig. 2B and C). This range, 29.4 ‰, essentially encompasses the entire range previously observed in mammalian bone collagen (see Nehlich, 2015). Given the ever increasing body of literature, these values reflect a variety of diets and environments, including areas impacted by both sea spray and marine precipitation (Lamb et al., 2023; McArdle et al., 1998; though see Guiry and Szpak, 2020 regarding the utility of $\delta^{34}S$ values for differentiating marine and terrestrial diets in sea spray-affected regions) as well as saltmarshes and wetlands (Guiry et al., 2021a), to areas further into the hinterland and away from the immediate coastline; locations where the taxa lived and/or ranged from.

Not many $\delta^{34}S$ values were obtained for humans ($n = 1$), ovicaprids ($n = 1$) and foxes ($n = 2$) (Fig. 2B and 2C; Table 2). Although these sample sizes are small and cannot be taken as representative, it is interesting to note that the one human (Sample 9387) had the lowest $\delta^{34}S$ value in the dataset. The $\delta^{34}S$ value of -13.7 ‰ not only reflects a terrestrial diet (i.e. $\delta^{34}S$ values lower than c. $+12$ ‰; Nehlich, 2015), which was also demonstrated by its $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 2A; Table 2), but shows that the individual did not consume marine sulfates, and likely did not reside in a wetland environment where plants reliant on sulfide-derived sulfur live (Guiry et al., 2021a). As such, the individual is undoubtedly non-local.

The ovicaprid (Sample 9374) and one of the foxes (Sample 9345) had $\delta^{34}S$ values of $+6.1$ ‰ and $+9.7$ ‰ (Fig. 2B and C; Table 2), which indicate a terrestrial diet and align with our interpretations of their $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 2A and 3; Table 2). While the $\delta^{34}S$ values demonstrated residency in an area unaffected by sea spray, they may have used saltmarshes (see Guiry et al., 2021a). In contrast, one of the foxes (Sample 9355) had a $\delta^{34}S$ value of $+9.8$ ‰ (Fig. 2B and 2C; Table 2), interpreted as a terrestrial diet based on Nehlich (2015). Despite consuming a substantial amount of marine foods as demonstrated by its $\delta^{13}C$ value (-13.2 ‰; Fig. 2A; Table 2), this seemingly unexpected $\delta^{34}S$ value likely demonstrates that the individual consumed animals that were sulfide-derived (Guiry et al., 2021a).

The cattle have a mean $\delta^{34}S$ value of $+3.5$ ‰ (SD = 8.7 ‰; $n = 5$), which is lower than the mean values of roe deer ($+7.1$ ‰; SD = 4.3 ‰; $n = 8$) and red deer ($+10.0$ ‰; SD = 7.0 ‰; $n = 8$) (Figs. 5 and 6; Tables 2 and 3). Although the $\delta^{13}C$ and $\delta^{15}N$ values of the herbivores demonstrated a terrestrial diet (Figs. 3 and 4; Table 2), the $\delta^{34}S$ values of at least one of the cattle (Sample 9359) and four red deer (Samples 9350, 9353, 9354 and 9368) indicated a marine diet (i.e. $\delta^{34}S$ values higher than c. $+12$ ‰; Nehlich, 2015; Figs. 5 and 6; Table 2). While these individuals may have consumed seaweed (see above), it is more likely that they had been feeding in an area, such as a saltmarsh, rich in marine sulfates (i.e. sea spray-affected; Guiry et al., 2021a).

Three roe deer (Samples 9341, 9364 and 9369) had $\delta^{34}S$ values lower than c. $+12$ ‰ (Nehlich, 2015), indicating a terrestrial diet, further supported by their $\delta^{13}C$ and $\delta^{15}N$ values (Figs. 3-6; Table 2). However, they likely had been grazing in a saltmarsh affected by sea spray as their $\delta^{34}S$ values were higher than c. $+10.0$ ‰ (Guiry et al., 2021a). The remaining cattle ($n = 4$), roe deer ($n = 5$) and red deer ($n = 4$) $\delta^{34}S$ values were lower than c. $+12$‰, indicating a terrestrial diet, and agree with their $\delta^{13}C$ and $\delta^{15}N$ compositions (Figs. 3 and 4; Table 2). While they had been feeding in areas without marine sulfates, they fall within the sulfide-derived range (Figs. 5 and 6). Of these, two cattle (Samples
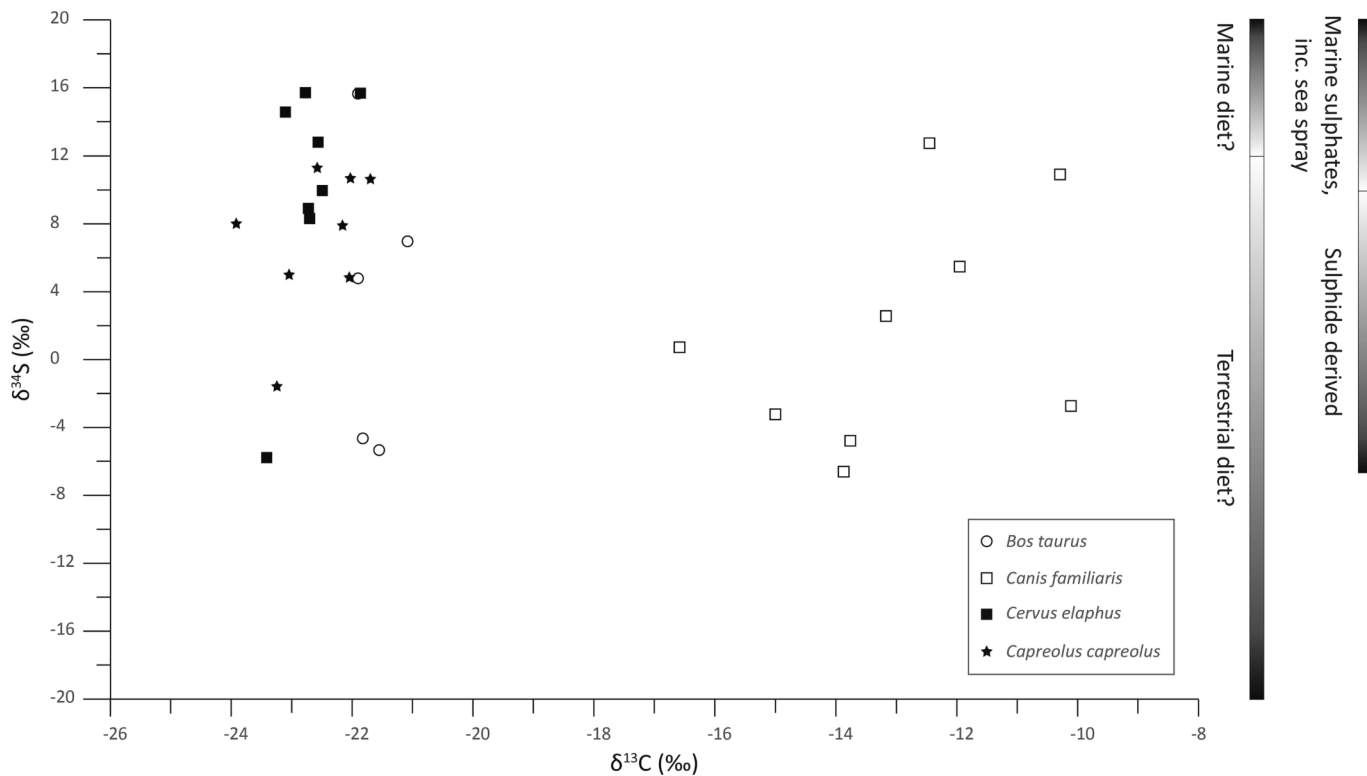
Fig. 5. δ¹³C and δ³⁴S values for taxa with more than three samples (see also Fig. 2).
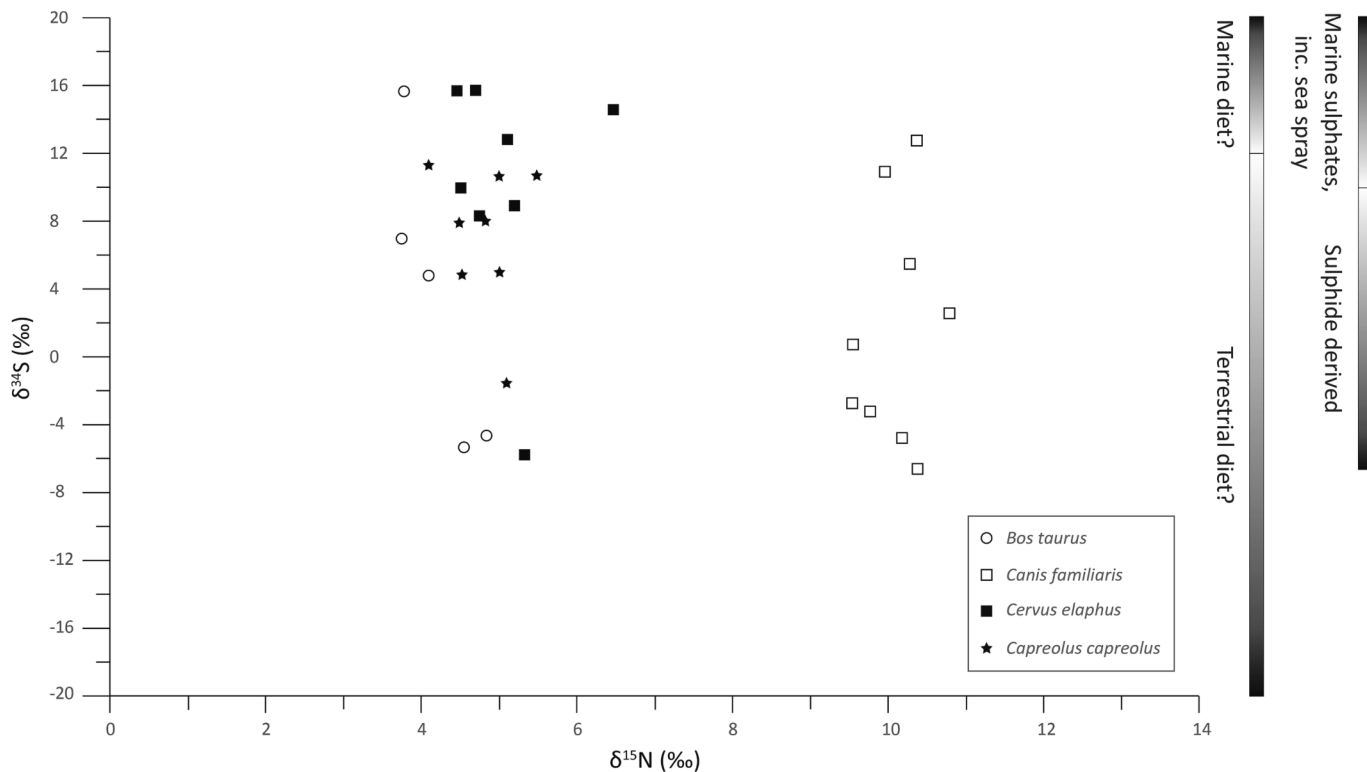
Fig. 6. δ¹⁵N and δ³⁴S values for taxa with more than three samples (see Fig. 2).

9373 and 9384), one red deer (Sample 9372) and one roe deer (Sample 9379) may have lived elsewhere as they cluster at the lower end of the range (see Figs. 5 and 6) and therefore may be non-local.

In comparison, the domestic dogs had a mean δ³⁴S value of + 1.7 ‰

(SD = 6.9 ‰; $n = 9$), which was lower than the herbivores (Figs. 5 and 6; Table 3). Only one dog (Sample 9360) had a δ³⁴S value higher than c. + 12 ‰ (Nehlich, 2015; Figs. 5 and 6; Table 2), corresponding to a marine diet, which was supported by its δ¹³C value of −12.5 ‰ (Fig. 4; Table 2).

A further specimen (Sample 9375) had a $\delta^{34}S$ value of + 10.9 ‰ (Figs. 5 and 6; Table 2) and as such likely fed in an area affected by sea spray, which was similarly supported by its $\delta^{13}C$ value of −10.3 ‰ (Fig. 4; Table 2). To our surprise, three dogs (Samples 9358, 9376 and 9382) had $\delta^{34}S$ values of + 5.5 ‰, +2.6 ‰ and + 0.7 ‰ (Figs. 5 and 6; Table 2). While these $\delta^{34}S$ values correspond to terrestrial diets according to Nehlich (2015), their $\delta^{13}C$ values of −12.0 ‰, −13.2 ‰ and −16.6 ‰, indicate the consumption of marine resources to varying degrees (Fig. 4; Table 2). The remaining specimens (Samples 9370, 9383, 9385 and 9386) had the lowest $\delta^{34}S$ values among the dogs, −3.2 ‰, −4.8 ‰, −2.7 ‰ and −6.6 ‰ respectively (Table 2), and are similarly interpreted as having terrestrial diets (Nehlich, 2015). They had also not fed in an area affected by sea spray (Nielsen, 1974; Norman et al., 2006), meaning that they may be non-local (Figs. 5 and 6). The $\delta^{34}S$ compositions, however, do not align with their $\delta^{13}C$ values of −15.0 ‰, −13.8 ‰, −10.1 ‰ and −13.9 ‰ (Table 2), demonstrating the consumption of varying quantities of marine foods. Consequently, these seven dogs (Samples 9358, 9370, 9376, 9382, 9383, 9385 and 9386) likely consumed animals that were sulfide-derived (Guiry et al., 2021a), for instance fish which reside in seagrass meadows (Guiry et al., 2021b).

4.3. Syltholm II and its place in the Neolithisation process

What then, do the stable isotope compositions tell us about the process of Neolithisation and the role of Syltholm II in it? Whilst it would be useful to know the chronological position of the analysed specimens relative to one-another, we are not hamstrung in this regard. This is due to the fact that we know the Syltholm Fjord sites, at least in part, represent the activities of persisting foragers during the EN (Jensen and Sørensen, 2023). This essentially removes the chronological border between the Mesolithic and the Neolithic as conventionally imagined and in itself raises questions regarding the EN economy at the site.

The overall herbivore data indicates the presence of a variety of terrestrial habitats on Lolland during the Neolithisation process and the deer show expected patterns of variation indicative of both forested and open environments. The cattle must be chronologically Neolithic (i.e., after *c.* 4000 cal BC, cf. Aaris-Sørensen, 1999) as they were introduced onto the island around this time. Their presence in the assemblage clearly means there is farming occurring somewhere in the landscape. Their diets are tightly controlled similar to other EN southern Scandinavian cattle and indicate that the animals were raised in open terrain (Gron, 2020; Gron and Rowley-Conwy, 2017; Noe-Nygaard et al., 2005). The same cannot be said for the ovicaprids however, which appear to have either been forest fed or had escaped into the forest themselves.

Despite their tightly controlled diets, as demonstrated by their $\delta^{13}C$ and $\delta^{15}N$ isotope compositions, the cattle likely originated from a number of different local areas, including location impacted by sea spray, saltmarshes and wetlands where plants reliant on sulfide-derived sulfur live (Guiry et al., 2021a). There is a similar diversity among the wild deer which would seem to indicate that hunting took place in multiple locations, including saltmarshes and wetlands and at similar locations where the cattle were grazing. An alternative explanation could be that the wild deer were being hunted alongside escaped or feral cattle at these locations reflecting a forager way of life that was continuing in a similar fashion as it did in the Late Mesolithic (e.g. Gron, 2023).

Whatever the case, the dogs are intermediate and have a more restricted range of $\delta^{34}S$ values than the cattle or red deer. This could mean that the dogs are moving between the different local areas, such as saltmarshes and wetlands, or consuming resources either rich in marine sulfates or sulfide-derived (Guiry et al., 2021a), for instance fish living in seagrass meadows (Guiry et al., 2021b). However, their predominantly marine diets (with one exception) under a canine surrogacy approach (see Guiry, 2012) indicates that these dogs accompanied groups of people eating a substantial amount of marine foods. So, any inland forays may have been brief and potentially emanating from settlements close to the coast, hinting at a continuing subsistence strategy that resembles the collector type (Binford, 1980). Interestingly, the one human sample had the lowest $\delta^{34}S$ value in the dataset, which is inconsistent with the $\delta^{34}S$ compositions of wild and domestic taxa – presumably reflecting the local area surrounding Sylholm Fjord (Fig. 2). Moreover, the mean $\delta^{13}C$ value of −20.9 ‰ (SD = 0.2 ‰; $n = 3$), indicating the consumption of terrestrial foodstuffs, contrasts markedly with all but one of the dogs. Although these remains have not been directly dated, their isotopic compositions correspond well with a much larger dataset obtained from Early Neolithic individuals (see Fischer et al., 2007), and likely represent non-local farmers.

The stable isotope data from the domestic animals show interesting patterns of variation that indicate that some of the specimens in the assemblages were likely not raised locally. It is therefore possible that a number of animals were brought into the area, by trade or off-site hunting. This lends insight into the functionality of the Syltholm Fjord area. Syltholm II is only one small component of a much larger archaeological complex, the excavated part of which extends over 1000 m E-W and contains many individual sites (Groß and Rothstein, 2023). As discussed above, people with hunter-gatherer ancestry apparently survived for several centuries alongside immigrant farmers (Jensen et al., 2019). Such a genetic duality was possibly paralleled in cultural and animal husbandry duality: older osseous artefact types continued to be made when new forms were implemented (Chaudesaigues-Clausen, 2023). Furthermore, small samples of suid mandibles suggest that wild boar bones were mainly deposited at the site of Syltholm II, while 300 m away at the archaeologically contemporary site of Syltholm X there are domestic pigs in the assemblage (Rowley-Conwy, 2023). Future detailed studies must show whether both areas were part of the same or different settlements. Finally, non-domestic 'ritual' depositional practices of an Ertebølle manner continued into Neolithic involving items originating from both cultural traditions (Sørensen, 2023).

Under such circumstances it becomes impossible to view Syltholm II (MLF00906-III) as a site with a single 'site economy'. Multiple economic activities were carried out in the area, and traces of many of these appear at Syltholm II. The Syltholm Fjord area evidently acted as a communal locale for people with both Mesolithic and Neolithic economies. The apparent genetic, cultural and animal husbandry duality has led to a highly complex multi-stranded set of archaeological depositions. Thus the analysed animals at Syltholm II do not point to a function of the site solely based on farming as at, for instance, Havnelev on the island of Zealand, Denmark (Gron, 2020; Nielsen, 1994). Also of interest is the fact that the ovicaprid diets do not seem to reflect any sort of specific management strategy; there is no pattern to their values relative to the other herbivores. Given the much less variable range of the $\delta^{34}S$ values of the roe deer and the domestic dogs, it is hard to imagine the range of variation seen in both the red deer and cattle being representative of any single locality, let alone Syltholm II and environs.

5. Conclusions

The overall picture on the basis of the $\delta^{34}S$ compositions therefore is indicative of human mobility to a number of locations in the area surrounding the Syltholm Fjord, including zones impacted by sea spray, saltmarshes and wetlands, where wild deer and fox hunting occurred. The cattle were clearly tightly controlled for the majority of their lives but were likely raised in multiple places, including sea spray-affected areas, saltmarshes and wetlands. Dogs were probably brought on hunting forays, and were predominantly fed a marine diet, including foodstuffs that were sulfide-derived as demonstrated by their variable $\delta^{34}S$ values.

Within the larger discourse regarding the transition to agriculture in southern Scandinavia, Syltholm II has several lessons to teach. Firstly, that the recent developments in our understanding of the Neolithisation process will force a reconsideration of all past and new data regarding the transition in the region (see Groß and Rothstein, 2023). In the case of

this dataset, it forefronts alternative interpretations of the past events that are represented by the domestic animal data. Secondly, these developments allow us to consider previously less-conceivable scenarios. In the case of Syltholm II, the likely diverse origins of the cattle weaken arguments for substantial active local husbandry. If those undertaking activities at Syltholm II were in fact persistent foragers (alternatively, "culturally Mesolithic foragers"), then the cattle were most likely obtained from the first farmers, either through trade, raiding, or hunting.

Lastly, this is how we see it now, and not necessarily reality. However, it is a good start in an attempt to understand what was a very dynamically changing cultural and economic landscape. It underscores that we are entering an exciting time in the study of the southern Scandinavian Neolithisation process. The prospect of prolonged contact between the last foragers and the first farmers is an enticing one, and the stable isotope evidence presented above is just one aspect of the story, but an important one.

CRediT authorship contribution statement

Kurt J. Gron: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. **Darren R. Gröcke:** Methodology, Validation, Formal analysis, Investigation, Data curation. **Daniel Groß:** Resources, Writing – original draft, Writing – review & editing. **Peter Rowley-Conwy:** Funding acquisition, Supervision, Writing – original draft, Writing – review & editing. **Harry K. Robson:** Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration. **Janet Montgomery:** Writing – original draft, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data are contained in the manuscript

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