



Research



Cite this article: Windle M, Pleuger-Dreibrodt S, Clark JK, Bayarsaikhan J, Taylor W, Piezonka H. 2025 Multi-species entanglements and stable isotope signals ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in modern reindeer herding communities of boreal northeast Asia. *Phil. Trans. R. Soc. B* **380**: 20240203. <https://doi.org/10.1098/rstb.2024.0203>

Received: 11 November 2024

Accepted: 25 March 2025

One contribution of 17 to a theme issue
'Unravelling domestication: multi-disciplinary
perspectives on human and non-human
relationships in the past, present and future'.

Subject Areas:

ecology, ecosystem

Keywords:

dietary isotopes, multi-species, North Asia,
reindeer domestication, Indigenous Knowledge,

Author for correspondence:

Morgan Windle
e-mails: morgan.windle@fu-berlin.de;
morganmwindle@gmail.com

Electronic supplementary material is available
online at <https://doi.org/10.6084/m9.figshare.c.7747672>.

Multi-species entanglements and stable isotope signals ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in modern reindeer herding communities of boreal northeast Asia

Morgan Windle¹, Sarah Pleuger-Dreibrodt², Julia K. Clark³, J. Bayarsaikhan⁴, William Taylor⁵ and Henny Piezonka⁶

¹Cluster of Excellence ROOTS, Kiel University, Kiel, Schleswig-Holstein, Germany

²School of History Classics and Archaeology, University of Edinburgh, Edinburgh, UK

³Nomad Science, Ulaanbaatar, Mongolia

⁴Institute of Archaeology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia

⁵Department of Anthropology, University of Colorado Boulder, Boulder, UK

⁶Free University of Berlin Institute of Prehistoric Archaeology, Berlin, Germany

MW, 0009-0006-2807-5268

Prevailing anthropocentric frameworks of animal husbandry in archaeological research are increasingly critiqued for their inability to capture the full spectrum of human–non-human systems. In west Siberia and northern Mongolia, reindeer herding communities practise an entwined multi-species lifeways with the subarctic boreal and forest ecosystems—but these practices lack secure archaeological chronologies and time depth in northeast Asia. Traces of reindeer herding and reindeer remains themselves are often under-represented in the depositional record, requiring alternative avenues for tracing the archaeology of reindeer herding. Here, we explore the potential of documenting these complex dynamics archaeologically through a proof-of-concept analysis of stable isotopic carbon and nitrogen in faunal bone collagen, which can represent a possible nexus of multi-species practices. In doing so, we seek to expand investigative potentials into both human and non-human community members, providing valuable, nuanced insights into past practices, hunter–herder interactions and domestication dynamics.

This article is part of the theme issue 'Unravelling domestication: multi-disciplinary perspectives on human and non-human relationships in the past, present and future'.

1. Introduction

For the past two centuries, historians, ethnographers and archaeologists have studied how fisher–hunter–gatherer communities in northern Eurasia integrated domestic reindeer (*Rangifer tarandus*) into their lifeways. Extensive work to understand the complex dynamics between humans and reindeer [1–7] and to pinpoint these relationships in the past [8–10] has led to a range of narratives on the origins of reindeer domestication in specific reindeer herding cultures. However, the exact time and place of reindeer domestication remain uncertain [11,12]. Today, reindeer are central to Indigenous fishing–hunting–gathering lifeway in northern Eurasia, as well as parts of Alaska, Canada and Greenland, serving as both domestic animals and wild game and shaping circumpolar societies since the Last Glacial Maximum [13,14].

Scholars increasingly show that domestication is a complex spectrum, with animals acting as agents within this continuum [15–17]. Domestication is a

continuing evolutionary process shaped by both natural and human-induced selection, where species can become genetically distinct, more dependent on humans for resources and exhibit phenotypic or behavioural changes [18]. However, it involves not just a genetic transformation but also a coevolutionary relationship, where humans and animals mutually influence each other through ongoing interaction, skills and knowledge [9]. While criteria such as genetic divergence and physical traits are debated as markers of domestication, the process is understood as both a biological and a cultural adaptation [15,16,18,19].

Reindeer are often referred to as ‘semi-domesticated’ [20–22], but this designation implies that domestication is incomplete or reaches a final stage, which does not align with current understandings of domestication (e.g. [15,16]). In reality, domestication is not a fixed endpoint but rather a fluid, ongoing process where humans and animals continue to influence each other’s abilities and survival strategies over time [9,16]. Labelling reindeer as ‘semi-domesticated’ therefore fails to capture this continuous interaction and coevolution. For this reason, here, we will refer to reindeer cohabiting with and being herded by communities as domesticated.

The current perspective on domestication is exemplified in the practices of reindeer herding, where humans and domestic reindeer adjust their respective behaviours to coexist within a shared, multi-species landscape. Reindeer herding often lacks conventional controls, emphasizing mutualism and symbiosis [1,23,24]. Reproductive controls do not follow a standard trajectory, as wild and herded reindeer can be intentionally interbred [25]. Herd composition can be highly variable, as it is not uncommon for working reindeer to join wild herds or vice versa [26]. Herders view domestic reindeer as community members, and ecological knowledge of reindeer dietary habits and behaviours plays a significant role in this mutualistic relationship [2,27], suggesting socio-cultural factors as key drivers in mutualistic systems. As more proxies for understanding past human–animal relationships emerge, such as soil biomarkers [28,29] and pathology analysis [30], it is crucial to integrate the diverse forms of human–reindeer cohabitation into other techniques for understanding the archaeology of domestication. The practices of reindeer herding communities could provide insights into the traceability of past human–reindeer cohabitation, deepening our understanding of animal integration into human lifeways.

Here, we examine the reindeer herding practices of the Sel’kup, and to a lesser extent the Khanty, in west Siberia, Russia, and the Tsaatan of northwest Mongolia. We aim to integrate a multi-species interpretive framework with stable isotope and ethnographic data. In doing so, we expand current biochemical indicators to allow for comparative analyses of archaeological and modern reindeer specimens while also testing the visibility of these mutualistic, multi-species relationships and considering broader implications regarding domestication.

(a) Multi-species frameworks in archaeology

In archaeological research non-human animals have often been considered through western [31], modern capitalistic [32] and highly anthropocentric lenses [33]. As a result, by studying animals as victims, symbolic objects or products in the archaeological record, they serve more as proxies for human action than representatives of an interspecies relationship [34,35]. The nature of these conceptual frameworks has had tangible impacts on narratives of human/non-human–animal relationships through time, for instance, in contributing to the secondary products’ revolution hypothesis [36,37], dichotomous wild versus domestic categorizations [38,39] and strict economic frameworks, particularly among hunter–fisher–herders [40,41]. Some scholars increasingly critique this framing of non-human animals, as it ineffectually captures the spectrum of roles which non-human animals have played in human societies [42–45].

Human and non-human–animal relationships are rarely two-way exchanges but exist in a network of relationships [46,47]. Newer frameworks examine interspecies rhythms [43,48] and prioritize non-human animals in their conceptual approaches [38,49]. These multi-species perspectives shift focus away from human dominance, situating the human past within a broader ecology of non-human actors and revealing key archaeological insights [43]. For example, isotopic analysis and ancient genomics of woolly dogs, such as those from the Coast Salish in the Pacific northwest, revealed how dogs shared human mobility and diets and participated in cultural practices and shaping human landscapes [50]. Similarly, reconstructing red deer antler use in Mesolithic tools and objects with such an interpretive lens highlighted human–animal entanglements beyond subsistence that contribute to the archaeological record [51]. Recognizing non-human animals as co-creators of the world has significant implications for understanding past societies, but archaeological methods must fully adapt to capture these dynamics.

(b) Dietary isotopes in human–animal archaeologies

One such analytical method is the use of stable isotopes, a valuable method for reconstructing past populations, migrations and cultural practices, which offers an alternative criterion for identifying domestic reindeer in the archaeological record without requiring robust archaeofaunal assemblages. While various isotopes are used in human–animal relationship reconstructions, such as strontium [52] and oxygen [53,54], stable isotopes of carbon and nitrogen could represent an effective avenue for identifying multi-species practices integral to systems like reindeer herding. Carbon and nitrogen stable isotopes are influenced by environmental factors, allowing for the reconstruction of bulk components in the diet of consumers. Where carbon stable isotopes help distinguish diets based on plant photosynthetic pathways and, to some extent, terrestrial versus marine food sources [55–58], nitrogen isotopes predominantly reveal protein sources in diets but also values influenced by local environmental conditions [59,60].

Generally, $\delta^{13}\text{C}$ values of C3 plants are sensitive to a wide range of environmental factors, which for example, can increase $\delta^{13}\text{C}$ values by 2–3‰ owing to water stress, high salinity soils and high elevation, whereas C4 plants exhibit slight variation

in $\delta^{13}\text{C}$ owing to environmental factors [61]. Variation between different organic tissues, different individuals/species and the influence of different diets can lead to larger offsets [62]. In research involving complex environmental food webs, it is the combined analysis with stable isotopic nitrogen which is key [63,64]. Stable isotopic nitrogen compositions of skeletal tissues are particularly impacted by the consumer's trophic level position, additionally indicating bulk terrestrial versus aquatic dietary components and different environmental factors impacting plants [65,66]. A stepwise enrichment of ^{15}N occurs with each upward shift in trophic level in the food chain [57,67], and the influential variables are well documented. Herbivore tissues are typically enriched in ^{15}N compared to the plants they consume, with ^{15}N levels increasing up the food chain [68]. Aquatic food chains also tend to be longer than terrestrial ones, incorporating a greater number of piscivorous trophic levels and allowing for the detection of aquatic resources as a dietary component in terrestrial consumers [57,69]. The presence of fishes in freshwater environments, such as those in boreal/taiga regions where reindeer are herded and which are vital resources for reindeer herding communities [70], as well as their diet and migration patterns between freshwater bodies, is reflected in the nitrogen values found in fish bone collagen.

The challenge of disentangling carbon and nitrogen isotopic signatures is because different tissues integrate isotopes over varied timescales. This makes tissue choice essential for reconstructing diet and ecology. Bone collagen reflects 10–20 years in an adult mammal owing to slow turnover, while in younger animals, it captures shorter, life-stage-specific periods, such as elevated values from milk intake during preweaning [71–74]. Other tissues like dental collagen, formed early, preserve juvenile dietary information, while antlers and keratin in hair and nails reflect shorter-term dietary inputs, from weeks to months, useful for tracking seasonal or episodic changes [72,74,75]. The animal's age at sampling is also important, as older animals show broader dietary histories, while younger animals' values reflect more immediate dietary influences, sensitive to rapid shifts. Both carbon and nitrogen values expressed in different species of wild or domestic herbivores depend on their dietary preferences and the seasonality of available food sources [72,76,77]. Bone collagen serves as an effective starting point for disentangling herded reindeer diets in North Asia, providing a broad baseline for dietary inputs that can reveal overarching trends and ecological and anthropological influences on reindeer populations.

Stable isotope analyses provide versatile tools and concepts that archaeologists, regardless of their theoretical approach, can effectively use [78]. A pluralistic approach in archaeology integrates diverse frameworks and bridges research divides to enhance understanding of human history [79,80]. Applying such frameworks to the interpretation of stable isotope data can improve insights into social negotiations that impact mobility and identity, as well as diet [81,82]. Multi-species anthropological perspectives in particular could be valuable interpretive lenses in stable isotope research for revealing the intricate relationships between humans, animals and their environments in such systems. When archaeofaunal remains are scarce, stable carbon and nitrogen isotope analysis of bone collagen provides a valuable proxy for reconstructing reindeer herding systems within specific environments and exploring interspecies interactions—particularly those that shape the community's diet.

(c) *Rangifer tarandus*

Rangifer tarandus (reindeer and caribou) are a medium-sized member of the Cervidae family and Arctic-adapted ungulates with a circumpolar distribution from the subarctic boreal forest to the high Arctic [83]. Their diet varies seasonally: in winter, they consume energy-rich, lichen-dominated forage, while in summer, they shift to a protein-rich diet consisting of fungi and large vascular plants such as herbs, shrubs and grasses [77].

During times of nutritional stress, which can be annual, reindeer also opportunistically consume bones, rodents, bird eggs, droppings and seaweed and kelp [84–87].

The migratory behaviour of *Rangifer* varies significantly depending on habitat, genetic lineage and environmental conditions. Some populations migrate extensively (50–1500 km), while others remain relatively sedentary, with movement patterns shaped by seasonal resource availability [88–90]. In spring, they frequently change pastures to follow the nutrient-rich new growth of plants, whereas in summer, movement is generally reduced [91,92]. The extreme climatic conditions of northern latitudes significantly influence their foraging strategies, as reindeer require high-quality forage to meet their physiological and metabolic demands [93,94]. This seasonal variation in diet and habitat drives the hyper-mobility of reindeer, with breeding females choosing higher-quality grazing areas to reduce nutritional stress [95].

In Arctic and subarctic regions, seasonal resource scarcity and nutritional stress shape the interactions between humans and animals [96–101], potentially influencing their cohabitation. Unlike other domesticated animals, reindeer follow similar seasonal cycles to their wild counterparts [102,103]. However, practices such as supplementary feeding or guiding reindeer to better pastures in North Asia may leave observable isotopic signals. These interventions benefit the reindeer and shape herders' daily activities, reflecting multi-species relationships. Isotopic studies of *Rangifer* provide valuable insights into human–reindeer interactions, including seasonal diets, movement and herding strategies [77,104,105].

Different herding strategies may influence isotopic signatures, with free-ranging reindeer potentially exhibiting dietary variability owing to access to diverse plant communities, while more intensively managed herds could display narrower isotopic ranges, though individual feeding choices may also play a role. Isotope signatures could also help trace reindeer's annual nutritional stress and community interventions to mitigate it, providing valuable insights into multi-species living. By comparing isotopic signals between herding systems, we can identify differences in seasonal movement, pasture management and anthropogenic influences, thereby providing deeper insights into how herders navigate environmental constraints and cultural practices in different ecological contexts.

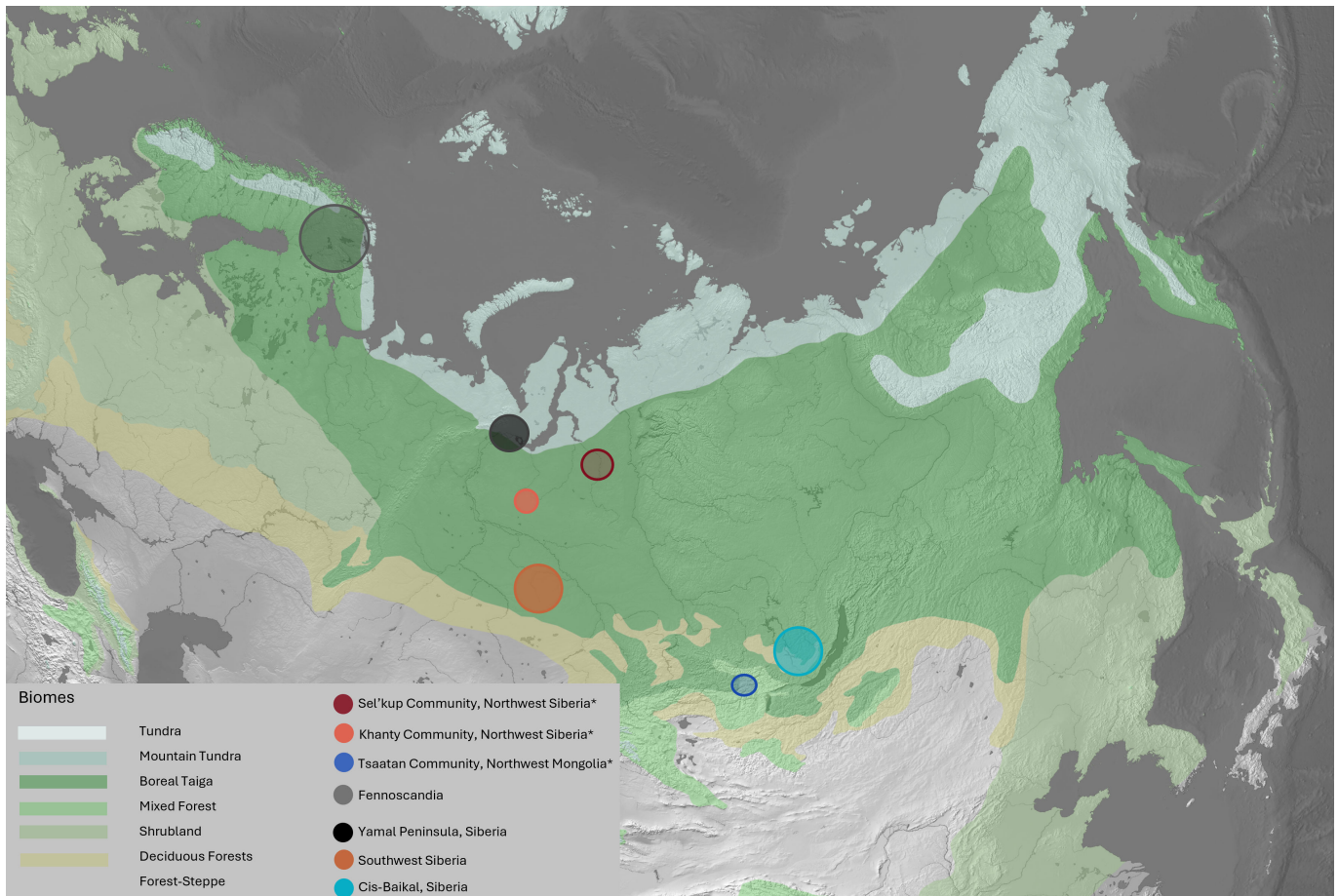


Figure 1. Location of study areas (Sel'kup community in west Siberia = red; Khanty = light orange; Tsaatan community in Khövsgöl, Mongolia = blue). Location of comparative studies from Fennoscandia, southwestern Siberia and Cis-Baikal Siberia, and the Yamal Peninsula (from studies [103,108–116]).

(d) Study area

Where treeless tundra habitats dominate the Arctic, the Subarctic can be defined by the approximate latitudinal extents for boreal ecosystems [106]. These boreal regions, collectively the 'taiga' in Eurasia, are a complex mosaic of habitats, changeable landscapes and widely dispersed human settlements [107]. Taiga landscapes are rich in resources, characterized by mixed coniferous forest, lichen, wetland vegetation and a variety of berries and mushrooms. The wild fauna encompasses large Arctic ungulates (elk/moose, wild reindeer), carnivores including bears and wolves, smaller mammals, birds (such as forest fowl/grouse, ptarmigan, etc.) and freshwater fishes. The foci of this study are two small-scale herding groups (Sel'kup and Tsaatan) and, to a lesser extent, a third (Khanty). These communities, either currently or historically engaged in reindeer herding, inhabit regions within the past and present extent of the Eurasian boreal (taiga) forest (figure 1). In collaboration with these communities, we recorded herd management practices and sampled animal bones from these two regions. See the electronic supplementary material, appendix A, for specific environmental descriptions of the regions.

(e) The Taz Sel'kup and Khanty of west Siberia

The northern Sel'kup are a subset of the Samoyedic language-speaking group whose name means 'forest people'. They migrated north from the Tomsk region to the Taz River in the seventeenth and eighteenth centuries owing to settler-colonial pressures, evicting local Enets groups from the area [117] and adopting local subsistence and cultural traits [118]. After arriving in this region, the socio-cultural and economic practices of the Sel'kup changed [70], resulting in substantial overlap in cultural features between neighbouring groups, including the neighbouring Khanty. Historically, Khanty groups have engaged in small-scale reindeer herding and hunter-fisher migrations along the river valleys of the middle and lower Ob and Irtysh rivers [119]. This study includes one sample from Khanty contexts. The northern (Taz) Sel'kup's primary adaptation to the area was the adoption of reindeer herding [117]; the incorporation of small-scale reindeer herding in which small herds of *ca* 10–70 head of deer are used almost exclusively for transport purposes, namely sled-pulling in bi-annual migrations to winter and summer campsites and during winter hunting expeditions, travelling along the frozen Taz River and into the tundra-taiga boundary area [70,118]. Their deer typically facilitate their fish-hunter-gatherer lifeways, slaughtering their domestic deer extremely rarely.

Taz Sel'kup use seasonal settlements and stations, with traditional dwelling structures including winter earth houses with ground-level floors (Sel'kup *poi-mot* = 'wooden house'), conical tents (Russian *chum*) for both summer and winter, and more recently introduced wooden log houses (which are increasingly replacing traditional structures) [118]. Management of reindeer

herds among Sel'kup communities is very free-range, with minimal controls placed on reindeer's mobility, particularly in summer. A key management tactic is the use of smokehouses/outdoor ovens to encourage reindeer to stay near summer settlements during the most intense of the summer insect harassment, which is attuned to reindeer's acute insect avoidance behaviours and encourages tameness and proximity to the summer settlement [117,119,120].

(f) Tsaatan of the northwest Mongolian 'taiga'

The forest zone in the far north of western Mongolia was historically the southernmost extension of the Eurasian taiga belt [121], is found around Lake Khövsgöl, the Darkhad Basin and the Sayan Mountains and extends into the Khentii mountains [122], forming a critical ecological zone. This taiga is divided into two, the Baruun (west) and Zuun (east) taiga, and is home to the reindeer herding Dukha ethnic group. The Dukha are ethnically Tuvan and share linguistic, cultural and historical ties with the broader Tuvan ethnic group in the Republic of Tuva, Russia, maintaining traditional practices that link them to their Siberian counterparts. Historically, they migrated through the Sayan Mountains until Soviet-era policies in the 1920s restricted their movement, and the closure of the Mongolia-USSR border in the 1940s further isolated them. By the 1980s, reindeer husbandry was nearly extinct, but efforts during Perestroika, combined with the importation of Siberian reindeer and veterinary reforms, helped revive the practice [123–126]. The Tsaatan community today constitutes around approximately 30 households/families, with approximately 500 people continuing the Tuvan traditional lifeways as pastoral people, living in conical *urts* [124,127]. Their reindeer husbandry today is part of an integrated economic mosaic that features aspects of both taiga- and steppe-based pastoralism, as well as small-scale hunting, fishing, gathering, agriculture, inter- and intra-regional trade and remunerated labour [125,126]. In the last century, Tsaatan lifeways have been strictly limited by the creation of national borders and the creation of the Ulaan Taiga Special Protected Area (UTSPA) [128].

2. Methods

(a) Ethnographic fieldwork

Fieldwork was conducted over multiple seasons from 2016 to 2023 (see the electronic supplementary material, appendices A and C), with a focus on documenting herding practices and their archaeological traceability. The team visited Taz Sel'kup summer and abandoned winter settlements, various Kazym Khanty communities in west Siberia, Russia and Tsaatan seasonal camps in the Baruun taiga, Mongolia. In addition to ethnographic methods like participant observation and informal interviews, the research included the collection of modern and recently excavated bone samples from summer settlements and camps. These samples, primarily from herded reindeer, were analysed to assess dietary patterns and husbandry practices. Local participants, either current or former herders, played a key role in guiding the research, which also involved archaeological surveys, photography and excavations, all conducted in collaboration with community partners (see the electronic supplementary material, appendices A and C, for full breakdown for field methods and sample origins).

3. Materials

To situate reindeer stable isotopic values not only within the two specific taiga environments, but also the larger food web, a range of other animal species (mammals, birds, fishes) were also sampled to better contextualize results and account for possible anthropogenic influence. We analysed samples from 34 animals: *Alces alces* ($n = 5$), *Falci pennis falci pennis* ($n = 1$), *Lepus timidus* ($n = 4$), *Esocidae/Percidae* sp. ($n = 5$) and *R. tarandus* ($n = 19$). We collected surface-scattered *Rangifer* bones from two Sel'kup summer settlements ($n = 5$), one Khanty summer settlement ($n = 1$) and four Tsaatan campsites ($n = 10$) (see the electronic supplementary material, appendix C, tables S1–S3).

Surface scatter reindeer bones were herded reindeer, according to community members. Two individuals were recently deceased herd members with known sex, age and health data, one of which (KIKK 122) was buried after death to avoid attracting predators to the area (see the electronic supplementary material, appendix B, figure S7).

Over the course of fieldwork in 2021, in addition to ethnographic activities, we excavated a semi-subterranean *poi-mot* on the Taz River which dated to the 1920s based on Sel'kup families and elders whose summer settlement was located next to the *poi-mot* and associated finds. Animal bones were present in two areas of the excavation, two pits on either side of the house platform, and all the seven samples came from pit 1 (see the electronic supplementary material, appendix B, figure S6). Only the *L. timidus* and three *R. tarandus* samples were from the 1920s *poi-mot*. With the exception of the 1920s samples, where the lifestyle of the reindeer and herders cannot be confirmed, all reindeer samples from west Siberia and Mongolia were from herded reindeer. All samples were collected over a series of ethnographic fieldwork seasons and contextualized through the documentation of herding practices (see the electronic supplementary material, appendix A).

(a) Sample selection

During the lifetime of reindeer, their bones are remodelled, like any animal [129], but nonetheless represent overarching trends in diet, whereas other tissues like antler isotopic values cannot represent more than a year of a reindeer's life owing to annual

shedding [75]. For these reasons, all samples came from adult animals to reduce potential variations driven by younger animals' bone turnover or nursing-related dietary signatures and to ensure consistency in time averaging. Where the age and sex of individuals were not known (via herder), adulthood was determined by confirming bones were fully fused and through tooth wear (particularly where the M3 was fully erupted and in wear; see the electronic supplementary material, appendix C, table S2). We excluded ribs and antlers from the range of skeletal elements, opting instead for mandibular bone and post-cranial limb bones which have lower turnover rates [130,131]. See the electronic supplementary material, appendix C, tables S2 and S3, for full list of sample, ages and values.

(b) Sample preparation and analysis

As all samples (surface collected, buried or ethnoarchaeological) date from the 1920s to 2022 and are intended for comparative analysis between modern and archaeological samples, the Suess effect was considered. The Suess effect suggests that an overall dilution of atmospheric $^{13}\text{CO}_2$ is the result of large amounts of fossil-fuel-derived CO_2 depleted in $^{13}\text{CO}_2$ admixing into the atmosphere [132]. Following [133], carbon results from samples from the 1920s *poi-mot* were adjusted, adding +0.5‰ and +2.0‰ to results from surface remains collected between 2020 and 2022, as animals with known year at death were within this data range, and bones collected from the surface are expected to be from within the last 5 years (see the electronic supplementary material, appendix B, table S3).

Samples were prepared and analysed at the Curt-Engelhorn-Zentrum Archäometrie gGmbH (CEZA). Demineralization was over 2–4 weeks in 10 ml of 0.5 M hydrochloric acid (HCl), first at 4°C and later at room temperature, followed by the removal of the surface and cancellous bone material with a dental drill. The acid solution was changed every 7 days until complete demineralization then rinsed to pH neutrality. As the samples were surface finds or buried bones humic acid removal was carried out in 10 ml of 0.1 M NaOH overnight at approximately 4°C, with the removal of NaOH through rinsing until pH neutrality. Collagen samples were then gelatinized in 4 ml of 0.001 M HCl (pH 3; 70°C, max. 48 h). Removal of insoluble particles was completed using Eze filters (Elkay; pore size approx. 60–90 µm) and lyophilization was completed over 48 h. Collagen samples were weighed into tin capsules (between 680 and 730 µg), and mass spectrometry was performed on triplicate samples. A vario ISOTOPE select elemental analyser (Elementar GmbH, Langenselbold) in carbon, nitrogen, and sulfur (CNS) mode at CEZA was used for combustion and determination of the carbon and nitrogen contents. Calibration of the element contents used internal software based on the calibration standards for elemental levels: sulfanilamide, United States Geological Survey (USGS) 43, USGS 40 and USGS 41a. An Isoprime visION isotope ratio mass spectrometer (Elementar GmbH, Langenselbold) determined the isotope ratios $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. An internal software calibrated the results using reference standards IAEA-CH-6, IAEA-CH-7, IAEA-N-1, IAEA-N-2, USGS 43, USGS 40 and USGS 41. Results use the delta notation in parts per thousand (‰) relative to the international standards Vienna PeeDee Belemnite (VPDB) for carbon and atmospheric nitrogen (AIR) for nitrogen.

The atomic C:N ratio is commonly used as a criterion for the degree of preservation of collagen purified for radiocarbon dating and stable isotope analysis: values between 2.9 and 3.6 are accepted as indicators of good collagen preservation [134,135], values outside this range were excluded from analysis (electronic supplementary material, table S2, appendix B).

We did not perform a lipid removal step because the skeletal remains were surface finds that had already undergone significant weathering leading to natural lipid degradation, and additional processing could have further compromised collagen integrity (see the electronic supplementary material, appendix A). Our elemental and isotopic data show no signs of lipid-related bias, and since comparative reindeer datasets (see [103]) also did not include lipid extraction, our results remain consistent and directly comparable to other published data.

(c) Statistics

The data results were checked for normality with the Shapiro–Wilk test using PAST software [136]. Student's *t*-tests were used when the means of two groups were tested for variance and normality was found. When more than two groups were compared, a one-way analysis of variance was followed by post hoc comparisons using Tukey range tests on all possible pairwise combinations. Differences were considered significant for *p*-values <0.05. Non-parametric tests compared our results for variance against published datasets, as normality was not found in all comparative regional datasets. When comparing our results against these external datasets Kruskal–Wallis and Dunn's *post hoc* pairwise combination comparisons were used. See the electronic supplementary material, appendix B, table S4, for all statistical results.

4. Results

(a) Ethnography

(i) Taz Sel'kup and Khanty

The Taz Sel'kup families we visited and collected samples from move twice a year between their summer and winter settlements, which are 8–20 km apart in the taiga, staying along the Taz River and its tributaries. That said, with the use of boats and extensive riverine systems, they are highly mobile and equally allow their reindeer free range. They indicated that past

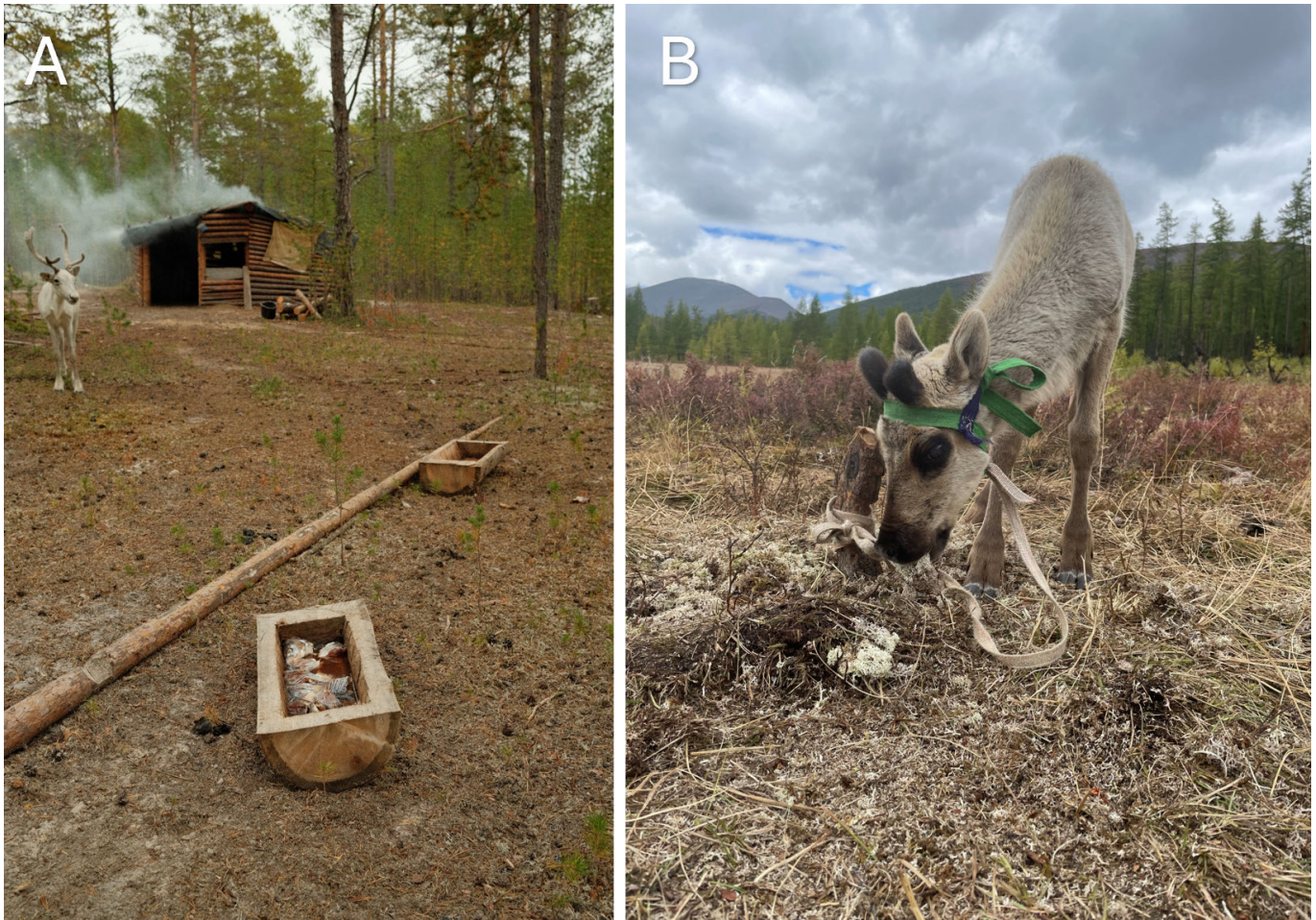


Figure 2. Examples of reindeer feeding across the study areas. (A) Fish feeding in troughs near reindeer house architectures among Sel'kup communities, and (B) lichen gathering and feeding to deer among Tsaatan. Photos by M. Windle.

generations migrated biweekly to monthly before Sovietization and the introduction of log houses. In addition to their summer and winter housing, other buildings on the summer settlements include stilted storage houses. Of particular note for this study are (i) reindeer smoke infrastructure and (ii) wooden storage containers, particularly for storing fish to feed the multi-species community in winter, including the reindeer (electronic supplementary material, appendix B, figure S2).

These constructions are specifically built and used for the small-scale reindeer husbandry in connection with the insects, namely 'smoke houses' as well as one or two smoke ovens inside. Alongside the smoke infrastructure is the placement of fish troughs by the houses and fires, which reindeer can consume throughout the day (figure 2).

Supplementary feeding was indicated as common among Sel'kup herders, primarily through fish feeding, both with troughs near smoke houses and hand feeding. The practice of fish feeding occurs year-round, according to the families we visited, to the extent that particular wooden storage facilities are built for storing fish for the deer. In our experience, fish feeding is done near to the smoke infrastructure to encourage the use of the smoke infrastructure, increase tameness around people, and provide extra nutrients to the deer. The fish feeding varied depending on the family, with two families tending to put fish in troughs on a weekly to monthly basis in summer and daily in the winter. By contrast, another family fed fish to their reindeer daily, with constant maintenance of the troughs, all year round. Procuring the fish is done in tandem with the daily fishing of Sel'kup family members to meet their own dietary needs, and typically the species of fish was the same as what was caught for the families, with the most common being pike (*Esox* sp.). Certain species are intentionally excluded and not fed to reindeer, namely spiny-finned fish such as perch (*Perca* sp.) as their spikes can upset the reindeer's stomachs.

The inclusion of the Khanty sample is used here because while the specimen was from a herded reindeer (according to the Khanty family), the community did not feed fish to their deer. This sample therefore represents the west Siberian taiga biome but without the influence of fish feedings, compared to samples from Sel'kup settlements.

(ii) Tsaatan (Dukha)

Tsaatan families we visited and collected samples from rely almost exclusively on their reindeer to facilitate their nomadic lifestyles, using them both as pack and riding animals for seasonal migrations and as everyday transport when herding deer or visiting neighbours. Additionally, reindeer milk serves as an important food resource. Tsaatan herded their reindeer daily to pasture, staking them near the *urts* during the night when they were not grazing. Reindeer management also involves practices such as hobbling or tying pairs of deer together at their antlers to limit mobility and simplify herding (electronic supplementary material, appendix B, figure S3). Seasonal camps are typically located in lower-elevation valleys or relatively flat, high-elevation

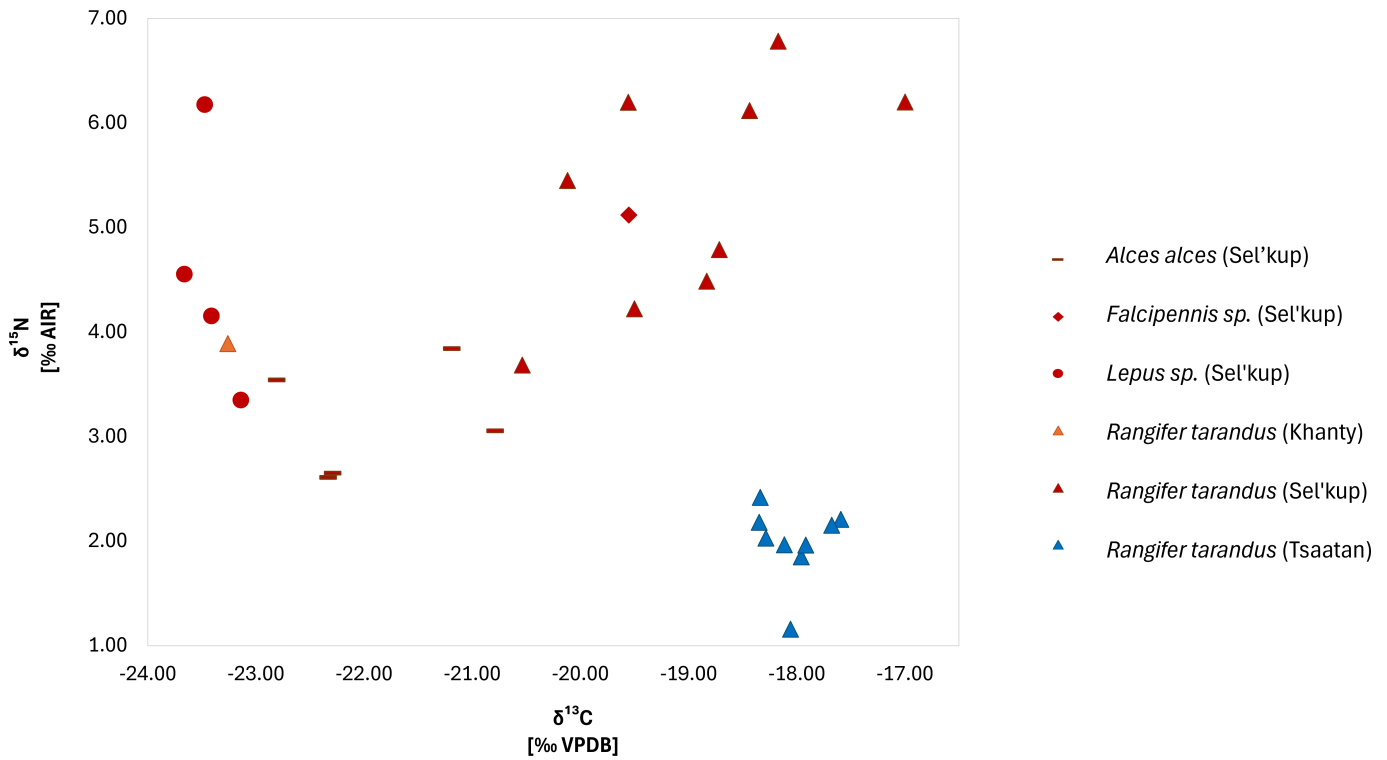


Figure 3. Carbon and nitrogen isotopic values from Sel'kup and Khanty communities, West Siberia and Tsaatan communities, northwest Mongolia.

terraces. Interviews suggest that open-air smoke infrastructures were used, similar to those of the Sel'kup, but this practice has fallen out of favour owing to declining insect populations. Instead, mobility plays a central role in their management, with reindeer husbandry practices built on the relationships between insects and reindeer.

Tsaatan families' mobility is highly variable, with camps being moved biweekly, monthly or seasonally. These moves typically occur between mountain valleys and the high-alpine tundra, more commonly in spring, summer and autumn. In winter, male family members cooperate in herding their deer. To supplement their reindeer's diet, they gather lichen throughout the year, with targeted lichen gathering occurring in winter. During this time, they do not migrate but instead move their herds between lichen fields and the winter settlement, where lichen is routinely gathered. When asked about intentionally feeding their reindeer, Tsaatan community members mentioned that they occasionally gather lichen from higher elevations in summer for young or injured deer (figure 2). By contrast, herders routinely collect and pile lichen for daily consumption by the reindeer in the winter. One family also indicated that urine (collected in pits or containers) is used year-round to attract deer near the *urts*, as it provides essential salt and minerals.

(b) Isotopic results

Of the 34 samples analysed, 29 fell within the accepted range of collagen of 2.9–3.6, whereas all fish samples had a range of C : N ratios from 3.8 to as high as 5.2, indicative of diagenetic changes and rendering them unreliable (electronic supplementary material, appendix B, table S2). No samples warranted exclusion owing to unreliable readings from the elemental analyser.

The corrected for Suess effect $\delta^{13}\text{C}$ values of samples from west Siberia ranged from -23.8 to -16.9 ‰ (mean -20.8 ± 2.4 ‰; figure 3). The $\delta^{13}\text{C}$ values of free-ranging domesticated reindeer ranged from -23.3 to -16.9 ‰ (mean -19.3 ± 2.3 ‰) and the single sample from the Khanty herd had the lowest carbon value. The range for other species from the Sel'kup area was as follows: -23.8 to -21.2 ‰ (mean -22.53 ± 1.1 ‰) for *A. alces*; -23.5 to -22.2 ‰ (mean -23.05 ± 0.6 ‰) for *Lepus* sp. samples; and the single *F. falci pennis* sample had a value of -19.6 ‰. In contrast to the west Siberian samples, Tsaatan reindeer had a far narrower range of carbon values from -18.4 to -17.6 ‰ (mean -18.1 ± 0.3 ‰) with, notably, a higher median than the west Siberian samples.

The $\delta^{15}\text{N}$ values of samples from West Siberia ranged from 2.6 to 6.8‰ (mean 4.5 ± 1.3 ‰; figure 3). The reindeer ranged from 3.7 to 6.8‰ (mean 5.2 ± 1.1 ‰) and the single sample from the Khanty herd was in the lower range with a value of 3.9‰. The range for other species from the Sel'kup area was as follows: 2.6 to 3.8‰ (mean 3.2 ± 0.6 ‰) for *A. alces*; 3.3 to 6.2‰ (mean 4.6 ± 1.2 ‰) for *Lepus* sp. samples; and the single *F. falci pennis* sample had a value of 5.1‰. As with the carbon values, Tsaatan reindeer had a far narrower range of nitrogen values from 1.2 to 2.4‰ (mean 2.0 ± 0.4 ‰).

Student's *t*-tests yielded a *p*-value of 2.44×10^{-7} between nitrogen values and a *p*-value of 0.027309 for carbon (electronic supplementary material, appendix B, table S4) of the two regions, demonstrating a significant difference between the west Siberian and Mongolian reindeer herds. Two potential clusters within the Sel'kup reindeer samples were identified (one cluster with lower $\delta^{15}\text{N}$ values, $n = 4$, and higher $\delta^{15}\text{N}$ values, $n = 5$, respectively), which we tested for significant difference using a Student's *t*-test. The intragroup clusters yielded a *p*-value of 0.0002 for stable isotopic nitrogen, demonstrating a statistically significant difference in the latter between the two Sel'kup reindeer clusters.

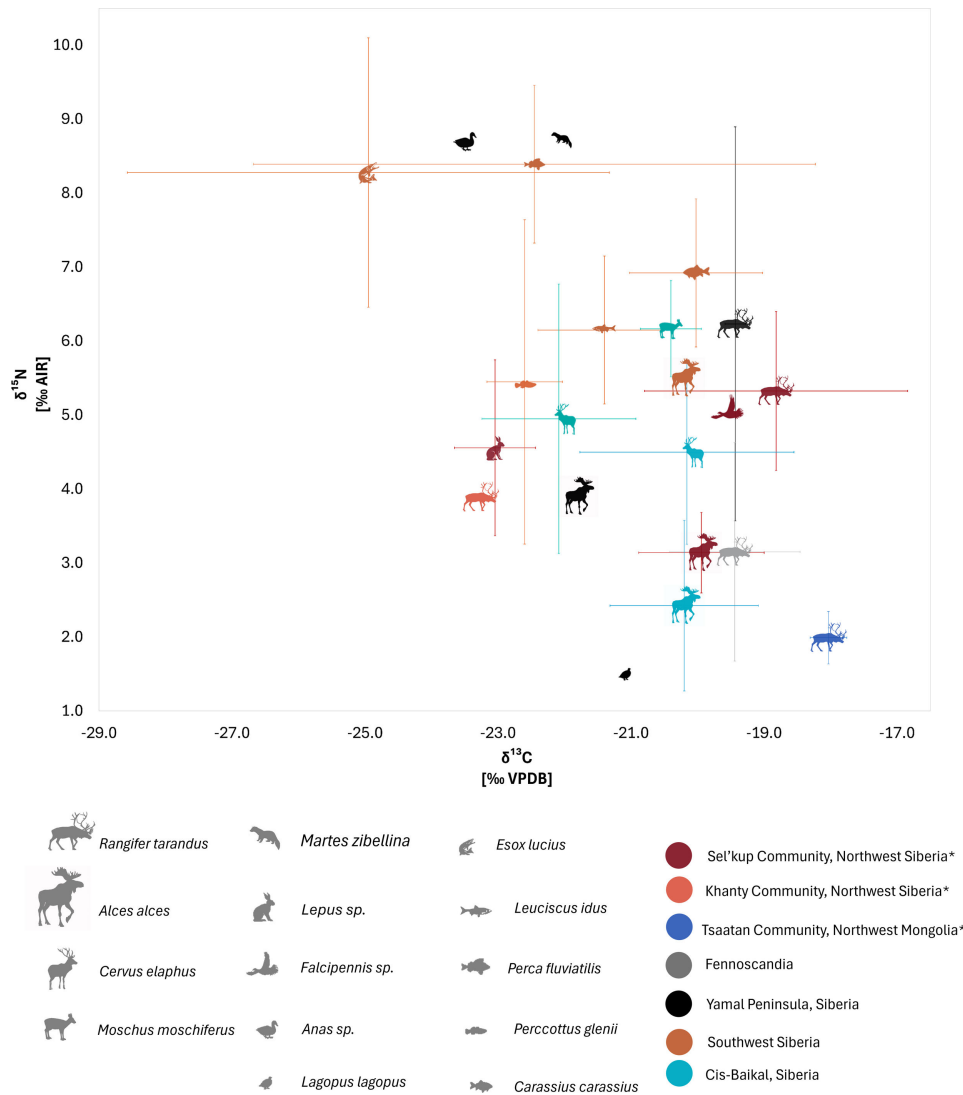


Figure 4. Summary graph showing the mean and standard deviation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from west Siberia* and Mongolia* and from Fennoscandia, southwest Siberia, Cis-Baikal Siberia, and the Yamal Peninsula, Siberia datasets (using data from studies [103,108–116]). *Original data.

5. Discussion

To help contextualize our results, we compiled published $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from regions where reindeer herding occurs and similar regional taxa in the study areas (figure 4; [103,108–116]). All modern comparative values were corrected for the Suess effect in their respective studies. However, we excluded non-adult, rib and antler samples to ensure better comparability with our dataset. Comparative reindeer samples are a combination of archaeological and modern contexts, the latter being from free-range, zoo and herded contexts [103,109,112,114–116]. In Fennoscandia, existing archaeological reindeer samples (*ca* 1200–1700 CE; [103,114–116]) had a $\delta^{13}\text{C}$ range of -22.0 to -17.7 (mean $-19.4 \pm 1.6\text{‰}$) and modern reindeer -21.0 to -18.3‰ (mean $-19.7 \pm 0.8\text{‰}$; [103,112]). $\delta^{15}\text{N}$ values were 1.1 to 8.5‰ (mean $3.4 \pm 1.6\text{‰}$).

Archaeological isotopic data from Siberian reindeer are limited, with available data from the Yamal Peninsula's Uist Polui site [109]. Here, $\delta^{13}\text{C}$ values ranged narrowly between -19.6 and -19.3‰ (mean $-19.4 \pm 0.2\text{‰}$), and $\delta^{15}\text{N}$ values spanned between 3.3 and 8.5‰ (mean $6.2 \pm 2.7\text{‰}$). We tested nitrogen variance between our west Siberian results and both the Fennoscandian and Yamal Peninsula data, finding significant differences ($p = 1.43 \times 10^{-5}$), specifically between our west Siberian, Mongolian and Fennoscandian reindeer datasets, as shown by Dunn's *post hoc* (electronic supplementary material, appendix B, table S4). However, no significant difference was found between west Siberian and Yamal samples ($p = 0.9$), though the Yamal data included only a few samples (electronic supplementary material, appendix B, table S4).

(a) Carbon

The $\delta^{13}\text{C}$ range among Siberian samples probably reflects the diverse species and biomes of their respective origins across the Cis-Baikal, Arctic tundra, and taiga regions of North Asia (figures 1 and 3). Notably, Mongolian Tsaatan reindeer had slightly higher $\delta^{13}\text{C}$ values (mean $-18.1 \pm 0.3\text{‰}$) than their Siberian counterparts (mean $-19.3 \pm 2.3\text{‰}$). This is probably, in part, owing to baseline isotopic differences between the C3-dominant ecosystems, shaped by local temperature and water availability. Regional plant isotope studies support these C3-specific variations, with taiga environments in Siberia (Sel'kup) characterized by marshy landscapes, while Mongolian (Tsaatan) samples originate from drier, mountainous regions.

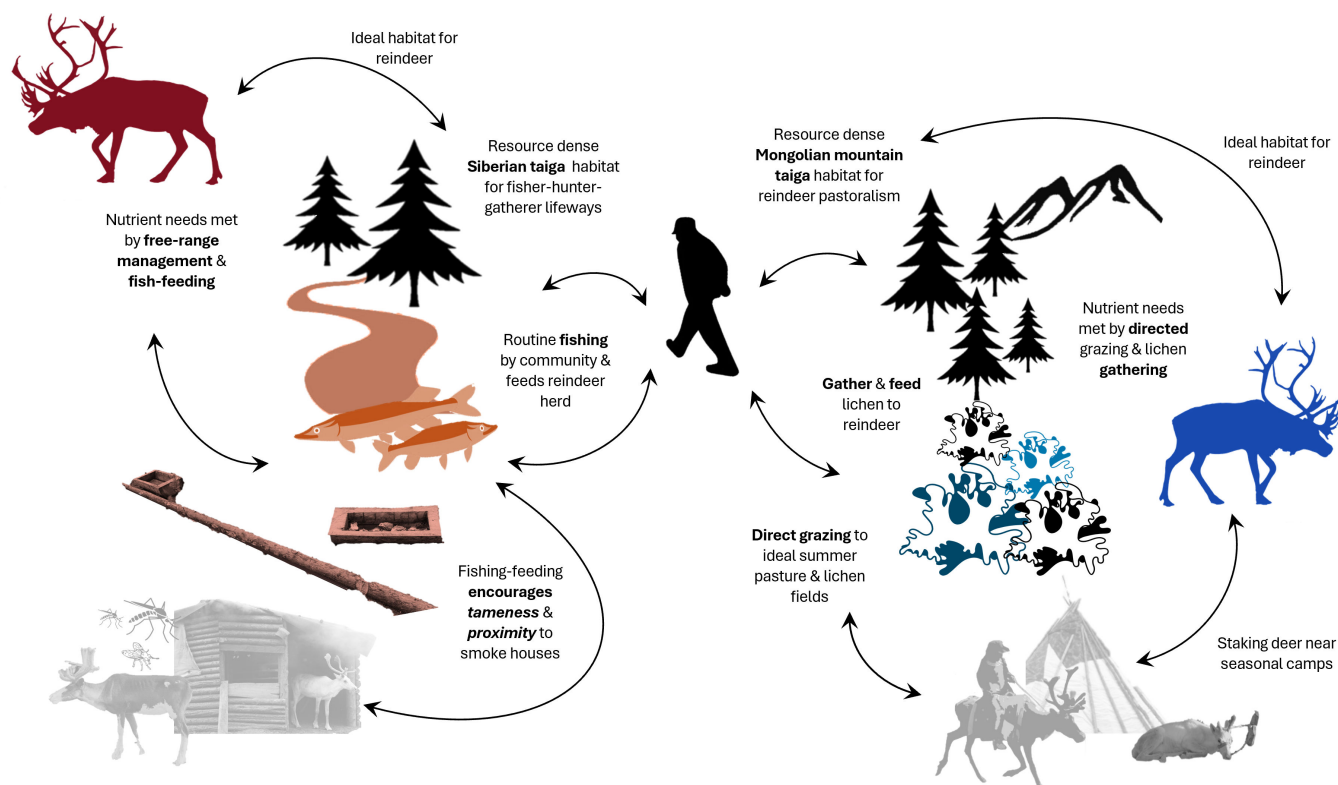


Figure 5. Tanglegram of described reindeer herding multi-species practices (red = est Siberia, blue = Mongolia).

The fish feeding we documented among Sel'kup herders could also influence $\delta^{13}\text{C}$ values in reindeer. Freshwater fishes exhibit highly variable $\delta^{13}\text{C}$ signatures depending on the aquatic ecosystem, ranging from values like terrestrial C3 plants to significantly enriched levels depending on a fish species' diet [137–140]. If fish feeding was substantial enough to impact $\delta^{15}\text{N}$ values, it is likely that it also influenced $\delta^{13}\text{C}$ values in the Sel'kup samples. That said, the precise influence on carbon cannot be easily disentangled from other influences using bulk collagen. Future studies incorporating isotopic baselines for local fish species could clarify this potential dietary contribution. Additionally, lichen consumption could significantly influence the reindeer $\delta^{13}\text{C}$ values. Lichen typically exhibits enriched $\delta^{13}\text{C}$ signatures compared to vascular plants, meaning that reindeer consuming high proportions of lichen could show slightly elevated $\delta^{13}\text{C}$ values relative to those primarily feeding on C3 vegetation [112,113]. Considering the practice of intentional gathering of lichen throughout the year to feed to their deer in Mongolia, though especially in winter, this could explain the slightly elevated $\delta^{13}\text{C}$ values among the Mongolian reindeer.

Herding strategies probably influenced the isotopic variation as well. In Siberia, Sel'kup reindeer herding involves minimal management, with herders rarely directing animals to specific pastures. Instead, they rely on smokehouses to guide the reindeer back to summer settlements (electronic supplementary material, appendix B, figure S1). This free-range approach allows animals to access diverse landscapes and plant varieties within the taiga. By contrast, Tsaatan herders in Mongolia operate within the UTSPA, which, while expansive, may offer different ecological conditions compared to broader free-ranging areas. Despite the spatial extent of the UTSPA, Tsaatan herders restrict reindeer mobility by hobbling pairs of reindeer, tying them to limit their range and guiding them to specific pastures near their summer campsites. This directed grazing strategy could reduce exposure to diverse vegetation types compared to Siberian herds. Additionally, while the UTSPA encompasses extensive terrain, and seasonal pasture rotation distances can be considerable, the pastures within park boundaries may still show limited vegetation diversity [141–143]. Expanding research on pasture degradation, particularly within restricted areas like the UTSPA, would enhance our understanding of stable isotopic carbon patterns and their link to herding practices.

(b) Nitrogen

The dramatic environmental changes (such as shifts in temperature and altitude) that reindeer experience owing to their grazing and migratory behaviours can influence their isotopic signatures. A primary example is the inverse relationship between altitude and isotopic values, where decreased lichen consumption lowers $\delta^{13}\text{C}$ values, while higher altitudes correspond with decreased $\delta^{15}\text{N}$ and increased $\delta^{13}\text{C}$ values [144]. ^{15}N values may also be affected by differences between Arctic and subarctic lichens and vascular plants [145,146]. While it is currently unclear how intra- and inter-annual variation in body $\delta^{15}\text{N}$ values (measured from blood, muscle and urine) translate into bone $\delta^{15}\text{N}$ values [147,148], our results reflect the different herds' environmental and dietary influences over several years.

Nutritional stress and starvation, which lead to the re-use of muscle protein, result in higher $\delta^{15}\text{N}$ [149]. As mentioned, this is common for reindeer in winter owing to limited access to high-quality graze [150,151]. However, it is unlikely that this effect alone accounts for the elevations observed in the Sel'kup samples, as seasonal nutritional stress would homogenize during bone collagen remodelling, resulting in lower overall enrichment signatures [104]. Year-round fish feeding, as documented in the

Sel'kup case, may contribute to $\delta^{15}\text{N}$ enrichment. When consulted alongside existing fish baselines (figure 4), fishes in Siberia exhibit a broad $\delta^{15}\text{N}$ range, overlapping with both omnivorous mammals and the Sel'kup reindeer samples (figure 4).

Our fieldwork showed that Sel'kup families do not engage in plant foddering but instead practise direct feeding. Although fish feeding has frequently been recorded as a winter practice [152], we found that it can occur year-round. Herders are acutely aware of their reindeer's nutritional needs and the frequent winter stress caused by extreme conditions. To mitigate this stress, they provide fish as a food source, either by placing troughs near smokehouses or by handfeeding (figure 2; also the electronic supplementary material, appendix C, figure S2). Beyond its nutritional role, ethnographic accounts suggest that fish feeding may also function as a herding technique to attract and tame reindeer, similar to the use of smoke or salt in reindeer management [2,153]. These overlapping motivations highlight the complex interactions that shape Sel'kup herding practices.

Comparing these findings to other managed reindeer populations provides further context for understanding isotopic enrichment. Elevated nitrogen values in modern Fennoscandian reindeer have been linked to industrial hay foddered with organic fertilizer [102]. In archaeological reindeer (thirteenth century CE), similar elevations were suggested to be the result of winter foddering of the reindeer with grasses, sedges and dried tree branches [103]. The mean $\delta^{15}\text{N}$ values from Fennoscandian studies (figure 4), interpreted as elevated, are statistically significantly lower than our Sel'kup samples as well as the archaeological reindeer bones samples from Uist Polui in the Yamal Peninsula, Siberia (figure 4). Compared to the Fennoscandian $\delta^{15}\text{N}$ values, the reindeer also sampled from Uist Polui are significantly enriched.

Notably, Losey and colleagues suggest that elevated $\delta^{15}\text{N}$ values in dogs may reflect human provisioning of fish [108]. Similarly, historical and modern fish storage practices among reindeer herders, including drying and smoking or preparation of fish soup [153], ensure a steady supply for both human and animal consumption. The persistence of these practices, as reflected in our ethnographic findings, suggests that fish feeding may have long-shaped isotopic signatures and remains integral to reindeer herding in North Asia.

The routine consumption of faunal proteins through the practice of fish feeding could be an important factor contributing to elevated values we see in Siberia, particularly when contextualized alongside nitrogen values of modern and archaeological fish (figure 4) from nearby regions. We suggest here that the elevated values of our Sel'kup reindeer samples are a result of this routine supplemental feeding of fish proteins by herders to reindeer and subsequently represent an indicator of the multi-species living in the region.

Finally, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differences between Tsaatan and Sel'kup reindeer reflect both diet and herding strategies. Tsaatan reindeer, managed within defined herding areas, show a narrower isotopic range, while free-ranging Sel'kup reindeer, with access to diverse forage and supplemental fish feeding, exhibit greater variation. Hobbling in Tsaatan herding may influence isotopic diversity, while Sel'kup mobility increases the exposure to varied vegetation and protein sources, potentially elevating $\delta^{15}\text{N}$ values. These findings highlight how herding practices interact with dietary intake and isotope compositions.

(c) Isotopes as an indicator of multi-species lifeways

Our results also show how isotopes can be representative of a nexus of multi-species actors and practices that can create a community (figure 5). In this case, a reindeer–fish–human interface co-creates the isotope record we encounter. Coupled with the mechanism that drives this, nutritional stress could have significant implications for understanding how reindeer domestication came to be. Notably, the influence of herding strategies, such as the directed grazing and mobility of Tsaatan reindeer versus the free-ranging Sel'kup herds, further shapes these isotopic signatures. The relationship between directed grazing, dietary diversity and supplemental feeding practices underscores the complex interplay between ecological adaptation and human management. Our understanding of animal responses to supplemental feeding is rapidly expanding, with studies demonstrating its long-term impacts on bird population dynamics and distribution [154], population densities, artificial selection of behavioural traits and herd health of ungulates [155,156]. Exposure to environmental and feeding conditions outside their normal habitat has led to extensive artificial selection across various orders, affecting Mongolian sheep [157]. Compensatory feeding like supplementing fish into the diet can have important implications. This is because through the combination of herder ecological knowledge, environment, and non-human species ecology, this specific niche-constructing practice arises and creates a feedback loop that encourages cooperation between herders and reindeer. This could then impact the selection pressures and subsequent domestication pathways for reindeer. Future directions should include larger studies of herder reindeer diets, look to other proteinaceous tissues to investigate the temporality of dietary shifts and incorporate other reindeer populations and herding communities across North Asia to expand on these results.

6. Conclusion

Stable isotope analysis is a powerful method for investigating human–animal interactions, particularly in regions with limited archaeological evidence. By examining stable carbon and nitrogen isotopes from reindeer bones, we can reconstruct dietary habits, mobility patterns and herding strategies, revealing the intricate multi-species relationships that shape reindeer herding systems. Our findings indicate that supplementary feeding practices, such as providing fish, leave distinct isotopic signatures that reflect human-mediated interactions with reindeer and their environments. Moreover, differences in herding strategies—such as the directed herding of Tsaatan pastoralists versus the free-ranging approach of Sel'kup herders—further influence isotopic variability by affecting dietary intake. These patterns underscore the role of multi-species interactions, where nutritional stress and compensatory feeding create feedback loops that may influence selection pressures and domestication pathways. This highlights the need for further research on reindeer diets across diverse populations and protein sources to

better understand dietary shifts over time. By integrating multi-species perspectives, stable isotope analysis provides a critical lens for interpreting how human–animal relationships actively shape archaeological records, offering valuable insights into reindeer domestication.

Ethics. Field protocols and animal remain sampling were approved by the Christian-Albrechts-Universität zu Kiel (CAU) ethics committee.

Data accessibility. Data can be accessed in the electronic supplementary material [158].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.W.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing - original draft, writing - review and editing; S.P.-D.: data curation, resources, validation, writing - review and editing; J.K.C.: project administration, resources, validation; J.B.: project administration; W.T.: writing - review and editing; H.P.: project administration, resources, supervision, validation.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This project has received funding from the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy ROOTS – Social, Environmental, and Cultural Connectivity in Past Societies (EXC 2150: 390870439).

Acknowledgements. We thank our Sel'kup and Tsaatan collaborators for their hospitality, guidance, and willingness to share their practices and lives with us. Without that, this work would not have been possible. Special thanks to the team at CEZA for their meticulous processing of the samples, with particular gratitude to Corina Knipper and Mila Sproß for their dedicated attention to sample preparation, processing, and their invaluable consultation throughout the study. Open access was additionally supported by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy (EXC 2150: 390870439).

References

- Stépanoff C, Marchina C, Fossier C, Bureau N. 2017 Animal autonomy and intermittent coexistences: North Asian modes of herding. *Curr. Anthropol.* **58**, 57–81. (doi:10.1086/690120)
- Stépanoff C. 2017 The rise of reindeer pastoralism in Northern Eurasia: human and animal motivations entangled: the rise of reindeer pastoralism in northern Eurasia. *J. R. Anthropol. Inst.* **23**, 376–396. (doi:10.1111/1467-9655.12612_1)
- Golovnev AV. 2016 The Arctic nomads: strategies of mobility. *Archaeol. Ethnol. Anthropol. Eurasia* **44**, 131–140. (doi:10.17746/1563-0110.2016.44.4.131-140)
- Baskin LM. 2003 River crossings as principal points of human/reindeer relationship in Eurasia. *Rangifer* **23**, 37. (doi:10.7557/2.23.5.1653)
- Golovnev AV. 1999 *Siberian survival: the nenets and their story*. Ithaca, NY: Cornell University Press. (doi:10.7591/j.ctv5qdg1n)
- Mirov NT. 1945 Notes on the domestication of reindeer. *Am. Anthropol.* **47**, 393–408. (doi:10.1525/aa.1945.47.3.02a00030)
- Donner K. 1933 The history of reindeer breeding. *J. R. Asiatic Soc. G. B. Ireland* **65**, 121–124. (doi:10.1017/S0035869X0007249X)
- Bjørklund I. 2013 Domestication, reindeer husbandry and the development of Sámi Pastoralism. *Acta Borealis* **30**, 174–189. (doi:10.1080/08003831.2013.847676)
- Losey RJ, Nomokonova T, Arzyutov DV, Gusev AV, Plekhanov AV, Fedorova NV, Anderson DG. 2021 Domestication as enskilment: harnessing reindeer in Arctic Siberia. *J. Archaeol. Method Theory* **28**, 197–231. (doi:10.1007/s10816-020-09455-w)
- Salmi AK. 2023 The archaeology of reindeer domestication and herding practices in northern Fennoscandia. *J. Archaeol. Res.* **31**, 617–660. (doi:10.1007/s10814-022-09182-8)
- Heino MT *et al.* 2021 Reindeer from Sámi offering sites document the replacement of wild reindeer genetic lineages by domestic ones in Northern Finland starting from 1400 to 1600 AD. *J. Archaeol. Sci.* **35**, 102691. (doi:10.1016/j.jasrep.2020.102691)
- Røed KH, Flagstad Ø, Nieminen M, Holand Ø, Dwyer MJ, Røv N, Vilà C. 2008 Genetic analyses reveal independent domestication origins of Eurasian reindeer. *Proc. R. Soc. B* **275**, 1849–1855. (doi:10.1098/rspb.2008.0332)
- Røed KH. 2005 Refugial origin and postglacial colonization of Holarctic reindeer and caribou. *Rangifer* **25**, 19–30. (doi:10.7557/2.25.1.334)
- Kvie KS, Heggnes J, Anderson DG, Kholodova MV, Sipko T, Mizin I, Røed KH. 2016 Colonizing the high Arctic: mitochondrial DNA reveals common origin of Eurasian Archipelagic reindeer (*Rangifer tarandus*). *PLoS ONE* **11**, e0165237. (doi:10.1371/journal.pone.0165237)
- Bogaard A *et al.* 2021 Reconsidering domestication from a process archaeology perspective. *World Archaeol.* **53**, 22. (doi:10.1080/00438243.2021.1954990)
- Losey RJ. 2022 Domestication is not an ancient moment of selection for prosociality: insights from dogs and modern humans. *J. Soc. Archaeol.* **22**, 131–148. (doi:10.1177/14696053211055475)
- Russell N. 2020 The domestication of anthropology. In *Where the wild things are now* (eds R Cassidy, M Mullin), pp. 27–48. London, UK: Routledge. (doi:10.4324/9781003087373-2)
- Zeder MA. 2020 Domestication: definition and overview. In *Encyclopedia of global archaeology* (ed. C Smith), pp. 3348–3358. Cham, Switzerland: Springer International Publishing. (doi:10.1007/978-3-030-30018-0_71)
- Clutton-Brock J. 1992 The process of domestication. *Mammal Rev.* **22**, 79–85. (doi:10.1111/j.1365-2907.1992.tb00122.x)
- Puputti AK, Niskanen M. 2009 Identification of semi-domesticated reindeer (*Rangifer tarandus tarandus*, Linnaeus 1758) and wild forest reindeer (*R. t. fennicus*, Lönnberg 1909) from postcranial skeletal measurements. *Mamm. Biol.* **74**, 49–58. (doi:10.1016/j.mambio.2008.03.002)
- Syroechkovski EE. 2000 Wild and semi-domesticated reindeer in Russia: status, population dynamics and trends under the present social and economic conditions. *Rangifer* **20**, 113. (doi:10.7557/2.20.2-3.1507)
- Helle T, Kojola I. 2006 Population trends of semi-domesticated reindeer in Fennoscandia — evaluation of explanations. In *Ecological studies reindeer management in northernmost Europe* (eds BC Forbes, M Bølter, L Müller-Wille, J Hukkinen, F Müller, N Gunsley), pp. 319–339. Berlin, Germany: Springer. (doi:10.1007/3-540-31392-3_16)
- Istomin KV, Dwyer MJ. 2010 Dynamic mutual adaptation: human–animal interaction in reindeer herding pastoralism. *Hum. Ecol.* **38**, 613–623. (doi:10.1007/s10745-010-9341-3)
- Stépanoff C. 2012 Human–animal 'joint commitment' in a reindeer herding system. *HAU J. Ethnogr. Theory* **2**, 287–312. (doi:10.14318/hau2.2.015)
- Brandišauskas D. 2019 *Leaving footprints in the taiga: luck, spirits and ambivalence among the siberian orochen reindeer herders and hunters*, vol. 1, 1st edn. London: Berghahn Books. See <https://www.jstor.org/stable/j.ctvss40w3>.
- Windle M, Kenig A, Piezonka H. 2021 Human–reindeer systems in the Taiga: preliminary results of ethnoarchaeological studies in the upper reaches of the river Taz. In *12th International Scientific Conference on Russian Cultural and Archaeological Research: Archaeology of Northern Russia*, pp. 277–284.

27. Anderson DG, Looovers JPL, Schroer SA, Wishart RP. 2017 Architectures of domestication: on emplacing human-animal relations in the North. *J. R. Anthropol. Inst.* **23**, 398–416. (doi:10.1111/1467-9655.12613_1)
28. Ęguez N, Makarewicz CA. 2018 Carbon isotope ratios of plant n-alkanes and microstratigraphy analyses of dung accumulations in a pastoral nomadic winter campsite (eastern Mongolia). *Ethnoarchaeology* **10**, 141–158. (doi:10.1080/19442890.2018.1510614)
29. Seitsonen O, Ęguez N. 2021 Here be reindeer: geoarchaeological approaches to the transspecies lifeworlds of the Sámi reindeer herder camps on the tundra. *Iskos* **24**, 124–145.
30. Salmi AK, Niinimäki S, Pudas T. 2020 Identification of working reindeer using palaeopathology and enthesal changes. *Int. J. Paleopathol.* **30**, 57–67. (doi:10.1016/j.ijpp.2020.02.001)
31. Žakula S, Živaljević I. 2018 The study of human-animal relations in anthropology and archaeology (I). *Glas Etnografskog Instituta SANU* **66**, 255–270. (doi:10.2298/GEI1802255Z)
32. Fitzpatrick A. 2022 Gesturing beyond bones: proposing a decolonised zooarchaeology. Conference: Approaches to Decolonising Research
33. Boyd B. 2017 Archaeology and human-animal relations: thinking through anthropocentrism. *Annu. Rev. Anthropol.* **46**, 299–316. (doi:10.1146/annurev-anthro-102116-041346)
34. Orton D. 2010 Both subject and object: herding, inalienability and sentient property in prehistory. *World Archaeol.* **42**, 188–200. (doi:10.1080/00438241003672773)
35. Hill E. 2013 Archaeology and animal persons: toward a prehistory of human-animal relations. *Environ. Soc.* **4**, s040108. (doi:10.3167/ares.2013.040108)
36. Sherratt A. 1981 Plough and pastoralism: aspects of the secondary products revolution. In *Economy and society in prehistoric europe: changing perspectives* (ed. A Sherratt), pp. 261–306. Cambridge, UK: Cambridge University Press. (doi:10.1515/9781474472562-009)
37. Greenfield H. 2010 The secondary products revolution: the past, the present and the future. *World Archaeol.* **42**, 29–54. (doi:10.1080/00438240903429722)
38. Hussain ST. 2024 Feral ecologies of the human deep past: multispecies archaeology and palaeo-synanthropy. *J. R. Anthropol. Inst.* **30**, 1062–1084. (doi:10.1111/1467-9655.14152)
39. Balasse M *et al.* 2016 Wild, domestic and feral? Investigating the status of Suids in the Romanian Gumelnița (5th mil. cal BC) with biogeochemistry and geometric morphometrics. *J. Anthropol. Archaeol.* **42**, 27–36. (doi:10.1016/j.jaa.2016.02.002)
40. Arnold JE, Sunell S, Nigra BT, Bishop KJ, Jones T, Bongers J. 2016 Entrenched disbelief: complex hunter-gatherers and the case for inclusive cultural evolutionary thinking. *J. Archaeol. Method Theory* **23**, 448–499. (doi:10.1007/s10816-015-9246-y)
41. Warren G. 2021 Is there such a thing as hunter-gatherer archaeology? *Heritage* **4**, 794–810. (doi:10.3390/heritage4020044)
42. Ogden LA, Hall B, Tanita K. 2013 Animals, plants, people, and things: a review of multispecies ethnography. *Environ. Soc.* **4**. (doi:10.3167/ares.2013.040102)
43. Pilaar Birch S. 2020 *Multispecies archaeology*, 1st edn. London: Routledge. See <https://www.routledge.com/Multispecies-Archaeology/Birch/p/book/9780367580858>.
44. Armstrong Oma K. 2010 Between trust and domination: social contracts between humans and animals. *World Archaeol.* **42**, 175–187. (doi:10.1080/00438241003672724)
45. Nyssönen J, Salmi AK. 2013 Towards a multiangled study of reindeer agency, overlapping environments, and human-animal relationships. *Arct. Anthropol.* **50**, 40–51. (doi:10.3368/aa.50.2.40)
46. Klenk N. 2018 From network to meshwork: becoming attuned to difference in transdisciplinary environmental research encounters. *Environ. Sci. Policy* **89**, 315–321. (doi:10.1016/j.envsci.2018.08.007)
47. TallBear K. 2015 An indigenous reflection on working beyond the human/not human. *GLQ J. Lesbian Gay. Stud.* **21**, 230–235.
48. Overton NJ, Hamilakis Y. 2013 A manifesto for a social zooarchaeology. Swans and other beings in the Mesolithic. *Archaeol. Dialogues* **20**, 111–136. (doi:10.1017/s1380203813000159)
49. Haughton M. 2024 Connecting posthumanist thinking with GIS practice: explorations of a prehistoric heathland landscape in Jutland, Denmark. *J. Archaeol. Method Theory* **31**, 227–250. (doi:10.1007/s10816-023-09603-y)
50. Lin AT *et al.* 2023 The history of coast salish ‘woolly dogs’ revealed by ancient genomics and indigenous knowledge. *Science* **382**, 1303–1308. (doi:10.1126/science.adi6549)
51. Conneller C. 2004 Becoming deer. Corporeal transformations at Star Carr. *Archaeol. Dialogues* **11**, 37–56. (doi:10.1017/s1380203804001357)
52. Knudson KJ, Price TD. 2007 Utility of multiple chemical techniques in archaeological residential mobility studies: case studies from Tiwanaku- and Chiribaya-affiliated sites in the Andes. *Am. J. Phys. Anthropol.* **132**, 25–39. (doi:10.1002/ajpa.20480)
53. Lazzarini N *et al.* 2021 The isotope record ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) of vertical mobility in incremental tissues (tooth enamel, hair) of modern livestock: a reference set from the Mongolian Altai. *Quat. Int.* **595**, 128–144. (doi:10.1016/j.quaint.2021.04.008)
54. Kirsanow K, Makarewicz C, Tuross N. 2008 Stable oxygen ($\delta^{18}\text{O}$) and hydrogen (δD) isotopes in ovicaprid dentinal collagen record seasonal variation. *J. Archaeol. Sci.* **35**, 3159–3167. (doi:10.1016/j.jas.2008.06.025)
55. Ambrose SH. 1986 Stable carbon and nitrogen isotope analysis of human and animal diet in Africa. *J. Hum. Evol.* **15**, 707–731. (doi:10.1016/s0047-2484(86)80006-9)
56. Ambrose SH, Norr L. 1993 Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In *Prehistoric human bone* (eds JB Lambert, G Grupe), pp. 1–37. Berlin, Germany: Springer. (doi:10.1007/978-3-662-02894-0_1)
57. Schoeninger MJ, DeNiro MJ. 1984 Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochim. Et Cosmochim. Acta* **48**, 625–639.
58. Schulting R, Richards M. 2016 Stable isotope analysis of Neolithic to late Bronze Age populations in the Samara valley. In *A bronze age landscape in the russian steppes: the samara valley project* (eds DW Anthony, DR Brown, OD Mochalov, AA Khokhlov, PF Kuznetsov), pp. 127–148. Cotsen Institute of Archaeology Press at UCLA. (doi:10.2307/j.ctvdjrq7b.13)
59. Amundson R, Austin AT, Schuur EAG, Yoo K, Matzek V, Kendall C, Uebersax A, Brenner D, Baisden WT. 2003 Global patterns of the isotopic composition of soil and plant nitrogen. *Glob. Biogeochem. Cycles* **17**, B001903. (doi:10.1029/2002gb001903)
60. Virginia RA, Delwiche CC. 1982 Natural ^{15}N abundance of presumed N_2 -fixing and non- N_2 -fixing plants from selected ecosystems. *Oecologia* **54**, 317–325. (doi:10.1007/bf00380000)
61. Tieszen LL. 1991 Natural variations in the carbon isotope values of plants: implications for archaeology, ecology, and paleoecology. *J. Archaeol. Sci.* **18**, 227–248. (doi:10.1016/0305-4403(91)90063-u)
62. DeNiro MJ, Epstein S. 1978 Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Et Cosmochim. Acta* **42**, 495–506.
63. Lee-Thorp JA. 2008 On isotopes and old bones. *Archaeometry* **50**, 925–950. (doi:10.1111/j.1475-4754.2008.00441.x)
64. Vogel JC, Van Der Merwe NJ. 1977 Isotopic evidence for early maize cultivation in New York State. *Am. Antiq.* **42**, 238–242. (doi:10.2307/278984)
65. Luo W, Wang X, Sardans J, Wang Z, Dijkstra FA, Lü XT, Peñuelas J, Han X. 2018 Higher capability of C_3 than C_4 plants to use nitrogen inferred from nitrogen stable isotopes along an aridity gradient. *Plant Soil* **428**, 93–103. (doi:10.1007/s11104-018-3661-2)
66. Wang C *et al.* 2014 Aridity threshold in controlling ecosystem nitrogen cycling in arid and semi-arid grasslands. *Nat. Commun.* **5**, 4799. (doi:10.1038/ncomms5799)
67. Minagawa M, Wada E. 1984 Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim. Et Cosmochim. Acta* **48**, 1135–1140.
68. Deniro MJ, Epstein S. 1981 Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim. Et Cosmochim. Acta* **45**, 341–351. (doi:10.1016/0016-7037(81)90244-1)

69. Schoeninger MJ, DeNiro MJ, Tauber H. 1983 Stable nitrogen isotope ratios of bone collagen reflect marine and terrestrial components of prehistoric human diet. *Sci. New Ser.* **220**, 1381–1383.
70. Piezonka H, Poshekhonova O, Adaev V, Rud' A. 2020 Migration and its effects on life ways and subsistence strategies of boreal hunter-fishers: ethnoarchaeological research among the Selkup, Siberia. *Quat. Int.* **541**, 189–203. (doi:10.1016/j.quaint.2019.07.005)
71. Jenkins SG, Partridge ST, Stephenson TR, Farley SD, Robbins CT. 2001 Nitrogen and carbon isotope fractionation between mothers, neonates, and nursing offspring. *Oecologia* **129**, 336–341. (doi:10.1007/s004420100755)
72. Balasse M, Bocherens H, Mariotti A, Ambrose SH. 2001 Detection of dietary changes by intra-tooth carbon and nitrogen isotopic analysis: an experimental study of dentine collagen of cattle (*Bos taurus*). *J. Archaeol. Sci.* **28**, 235–245. (doi:10.1006/jasc.1999.0535)
73. Martínez del Río C, Carleton SA. 2012 How fast and how faithful: the dynamics of isotopic incorporation into animal tissues. *J. Mammal.* **93**, 353–359. (doi:10.1644/11-mamm-s-165.1)
74. Zazzo A, Harrison SM, Bahar B, Moloney AP, Monahan FJ, Scrimgeour CM, Schmidt O. 2007 Experimental determination of dietary carbon turnover in bovine hair and hoof. *Can. J. Zool.* **85**, 1239–1248. (doi:10.1139/z07-110)
75. Stevens RE, O'Connell TC. 2016 Red deer bone and antler collagen are not isotopically equivalent in carbon and nitrogen. *Rapid Commun. Mass Spectrom.* **30**, 1969–1984. (doi:10.1002/rcm.7670)
76. Makarewicz CA. 2014 Winter pasturing practices and variable fodder provisioning detected in nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotopes in sheep dental collagen. *J. Archaeol. Sci.* **41**, 502–510. (doi:10.1016/j.jas.2013.09.016)
77. Drucker DG, Hobson KA, Ouellet JP, Courtois R. 2010 Influence of forage preferences and habitat use on ^{13}C and ^{15}N abundance in wild caribou (*Rangifer tarandus caribou*) and moose (*Alces alces*) from Canada. *Isotopes Environ. Health Stud.* **46**, 107–121. (doi:10.1080/10256010903388410)
78. Martínón-Torres M, Killick D. 2015 Archaeological theories and archaeological sciences. In *The oxford handbook of archaeological theory* (eds A Gardner, M Lake, U Sommer), pp. 1–17. Oxford, UK: Oxford University Press. (doi:10.1093/oxfordhb/9780199567942.013.004)
79. Hussain ST. 2019 The French-Anglophone divide in lithic research: a plea for pluralism in Palaeolithic Archaeology. Leiden University. <https://hdl.handle.net/1887/69812>.
80. Hussain ST, Will M. 2021 Materiality, agency and evolution of lithic technology: an integrated perspective for palaeolithic archaeology. *J. Archaeol. Method Theory* **28**, 617–670. (doi:10.1007/s10816-020-09483-6)
81. Makarewicz CA, Sealy J. 2015 Dietary reconstruction, mobility, and the analysis of ancient skeletal tissues: expanding the prospects of stable isotope research in archaeology. *J. Archaeol. Sci.* **56**, 146–158. (doi:10.1016/j.jas.2015.02.035)
82. Makarewicz CA. 2016 Toward an integrated isotope zooarchaeology. In *Isotopic landscapes in bioarchaeology* (eds G Grupe, GC McGlynn), pp. 189–209. Berlin, Germany: Springer. (doi:10.1007/978-3-662-48339-8_11)
83. Lin Z *et al.* 2019 Biological adaptations in the Arctic cervid, the reindeer (*Rangifer tarandus*). *Science* **364**, eaav6312. (doi:10.1126/science.aav6312)
84. Loginova OA, Belova LM. 2019 Food habits of northern deer, conducting their invasion by helminths. *Theory Pract. Parasit. Dis. Control* **14**, 318–322. (doi:10.31016/978-5-9902340-8-6.2019.20.318-322)
85. van der Wal R, Loonen MJJE. 1998 Goose droppings as food for reindeer. *Can. J. Zool.* **76**, 1117–1122. (doi:10.1139/cjz-76-6-1117)
86. Fellman I. 1910 *Handlingar och uppsatser angående finska lappmarken och lapparne i-iv*. Helsinki: Fin Litteratursällskapets Tryckeri.
87. Hansen BB, Lorentzen JR, Welker JM, Varpe Ø, Aanes R, Beumer LT, Pedersen ÅØ. 2019 Reindeer turning maritime: ice-locked tundra triggers changes in dietary niche utilization. *Ecosphere* **10**, e02672. (doi:10.1002/ecs2.2672)
88. Nieminen M. 1986 Chemical composition of the reindeer summer and winter food. *Rangifer* **6**, 96. (doi:10.7557/2.6.1-app.617)
89. Cavedon M *et al.* 2022 Genomic legacy of migration in endangered caribou. *PLoS Genet.* **18**, e1009974. (doi:10.1371/journal.pgen.1009974)
90. Bonar M, Anderson SJ, Anderson CR Jr, Wittemyer G, Northrup JM, Shafer ABA. 2022 Genomic correlates for migratory direction in a free-ranging cervid. *Proc. R. Soc. B* **289**, 20221969. (doi:10.1098/rspb.2022.1969)
91. Volkovitskiy A, Terekhina A. 2023 A microregional reindeer herding landscape in Yamal: patterns and dynamics of movements. *Pastoralism* **13**, 27. (doi:10.1186/s13570-023-00292-6)
92. Skarin A, Danell Ö, Bergström R, Moen J. 2008 Summer habitat preferences of GPS-collared reindeer *Rangifer tarandus tarandus*. *Wildl. Biol.* **14**, 1–15. (doi:10.2981/0909-6396(2008)14[1:shpogr]2.0.co;2)
93. Klein DR. 1990 Variation in quality of caribou and reindeer forage plants associated with season, plant part, and phenology. *Rangifer* **10**, 123. (doi:10.7557/2.10.3.841)
94. Mårell A, Edenius L. 2006 Spatial heterogeneity and hierarchical feeding habitat selection by reindeer. *Arct. Antarct. Alp. Res.* **38**, 413–420. (doi:10.1657/1523-0430(2006)38[413:shahfh]2.0.co;2)
95. Säkkinen H, Timisjärvi J, Eloranta E, Heiskari U, Nieminen M, Puukka M. 1999 Nutrition-induced changes in blood chemical parameters of pregnant reindeer hinds (*Rangifer tarandus tarandus*). *Small Rumin. Res.* **32**, 211–221. (doi:10.1016/s0921-4488(98)00184-9)
96. Ehlers L, Coulombe G, Herriges J, Bentzen T, Suito M, Joly K, Hebblewhite M. 2021 Critical summer foraging tradeoffs in a subarctic ungulate. *Ecol. Evol.* **11**, 17835–17872. (doi:10.1002/ece3.8349)
97. Klein DR. 1996 Arctic ungulates at the northern edge of terrestrial life. *Rangifer* **16**, 6. (doi:10.7557/2.16.2.1197)
98. Joly K, Gunn A, Côté SD, Panzacchi M, Adamczewski J, Suito MJ, Gurarie E. 2021 Caribou and reindeer migrations in the changing Arctic. *Anim. Migr.* **8**, 156–167. (doi:10.1515/ami-2020-0110)
99. Johnson CJ, Boyce MS, Case RL, Cluff HD, Gau RJ, Gunn A, Mulders R. 2005 Cumulative effects of human developments on Arctic wildlife. *Wildl. Monogr* **160**, 1–36. (doi:10.2193/0084-0173(2005)160[1:ceohdo]2.0.co;2)
100. Gmoshinski IV, Nikityuk DB. 2023 Arctic stress: mechanisms and experimental models. *Ann. Russ. Acad. Med. Sci.* **77**, 447–457. (doi:10.15690/vramn2209)
101. Nancarrow TL, Chan L. 2010 Observations of environmental changes and potential dietary impacts in two communities in Nunavut, Canada. *Rural Remote Health* **1370**. (doi:10.22605/rrh1370)
102. Nieminen M, Heiskari U. 1989 Diets of freely grazing and captive reindeer during summer and winter. *Rangifer* **9**, 17. (doi:10.7557/2.9.1.771)
103. Salmi AK, Fjellström M, Äikäs T, Spangen M, Núñez M, Lidén K. 2020 Zooarchaeological and stable isotope evidence of Sámi reindeer offerings. *J. Archaeol. Sci.* **29**, 102129. (doi:10.1016/j.jasrep.2019.102129)
104. Britton K. 2010 Multi-isotope analysis and the reconstruction of prey species palaeomigrations and palaeoecology. [Durham]: Durham University. <http://etheses.dur.ac.uk/216/> (accessed September 2024).

105. Britton K, Jimenez EL, Le Corre M, Renou S, Rendu W, Richards MP, Hublin JJ, Soressi M. 2023 Multi-isotope analysis of bone collagen of late pleistocene ungulates reveals niche partitioning and behavioural plasticity of reindeer during MIS 3. *Sci. Rep.* **13**, 15722. (doi:10.1038/s41598-023-42199-7)
106. Hoberg EP, Kutz S, Galbreath K, Cook J. 2003 Arctic biodiversity: from discovery to faunal baselines - revealing the history of a dynamic ecosystem. *J. Parasitol.* **1**, 89:584, 95.
107. Adaev V. 2007 Traditsionnaya ekologicheskaya kul'tura khantov i nentsyev zapadnoy sibiri. [Novosibirsk]: Institute of Archaeology and Ethnography SB RAS. <https://www.pribl.ru/item/375708> (accessed July 2023).
108. Losey RJ, Guiry E, Nomokonova T, Gusev AV, Szpak P. 2020 Storing fish?: a dog's isotopic biography provides insight into Iron age food preservation strategies in the Russian Arctic. *Archaeol. Anthropol. Sci.* **12**, 200. (doi:10.1007/s12520-020-01166-3)
109. Losey RJ, Fleming LS, Nomokonova T, Gusev AV, Fedorova NV, Garvie-Lok S, Bachura OP, Kosintsev PA, Sablin MV. 2018 Human and dog consumption of fish on the lower Ob river of Siberia: evidence for a major freshwater reservoir effect at the ust'-polui site. *Radiocarbon* **60**, 239–260. (doi:10.1017/rdc.2017.77)
110. Marchenko ZV, Syatko SV, Grishin AE. 2021 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope analysis of modern freshwater fish in the south of Western Siberia and its potential for palaeoreconstructions. *Quat. Int.* **598**, 97–109. (doi:10.1016/j.quaint.2021.06.006)
111. Katzenberg MA, McKenzie HG, Losey RJ, Goriunova OI, Weber A. 2012 Prehistoric dietary adaptations among hunter-fisher-gatherers from the little sea of lake Baikal, Siberia, Russian federation. *J. Archaeol. Sci.* **39**, 2612–2626. (doi:10.1016/j.jas.2011.08.010)
112. Dury JPR, Eriksson G, Fjellström M, Wallerström T, Lidén K. 2018 Consideration of freshwater and multiple marine reservoir effects: dating of individuals with mixed diets from Northern Sweden. *Radiocarbon* **60**, 1561–1585. (doi:10.1017/rdc.2018.78)
113. Weber AW, Link DW, Katzenberg MA. 2002 Hunter-gatherer culture change and continuity in the middle Holocene of the Cis-Baikal, Siberia. *J. Anthropol. Archaeol.* **21**, 230–299. (doi:10.1006/jaar.2001.0395)
114. Fjellström M, Eriksson G, Angerbjörn A, Lidén K. 2020 Approaching historic reindeer herding in Northern Sweden by stable isotope analysis. *J. Nord Archaeol. Sci.* **19**, 63–75.
115. Fjellström M. 2023 Fragmented reindeer of Ställo foundations: a multi-isotopic approach to fragmented reindeer skeletal remains from Adámvallda in Swedish Sápmi. In *Broken bodies, places and objects new perspectives on fragmentation in archaeology* (eds A Sörman, N Noterman, M Fjellström), pp. 157–172. London, UK: Routledge. (doi:10.4324/9781003350026-12)
116. Salmi AK, Äikäs T, Fjellström M, Spangen M. 2015 Animal offerings at the Sámi offering site of Unna Saiva – changing religious practices and human–animal relationships. *J. Anthropol. Archaeol.* **40**, 10–22. (doi:10.1016/j.jaa.2015.05.003)
117. Golovnev A, Tuchkova NA. 2005 Sel'kupy: khozyaystvo. In *Narody zapadnoj sibiri. khanty. mansy. sel'kupy. entsy. nganasany. kety* (eds I.N. Gemuev, VI Molodin, ZP Sokolova), pp. 317–328. Moscow: Nauka.
118. Piezonka H, Adaev V, Kenig A, Rud' A, Windle M. 2024 Household and settlement organization of mobile hunter-fisher-reindeer herders in western Siberia: an ethnoarchaeological study. In *Mobile pastoralist households: archaeological and ethnoarchaeological perspectives* (ed. JL Houle), pp. 120–158. New York: Berghahn Books. (doi:10.1515/9781805396734-007)
119. Kenig A. Etnoarkheologiya Kak Metod Arkheologicheskikh Rekonstruktsiy (Na Primere Tazovskikh Sel'kupov). See <https://www.elibrary.ru/item.asp?id=19725192> (accessed 7 March 2024).
120. Groß D *et al.* 2019 Adaptations and transformations of hunter-gatherers in forest environments: new archaeological and anthropological insights. *Holocene* **29**, 1531–1544. (doi:10.1177/0959683619857231)
121. Klinge M, Dulamsuren C, Erasmi S, Karger DN, Hauck M. 2018 Climate effects on vegetation vitality at the treeline of boreal forests of Mongolia. *Biogeosciences* **15**, 1319–1333. (doi:10.5194/bg-15-1319-2018)
122. Dulamsuren C, Hauck M. 2008 Spatial and seasonal variation of climate on steppe slopes of the northern Mongolian mountain Taiga. *Grassl. Sci.* **54**, 217–230. (doi:10.1111/j.1744-697X.2008.00128.x)
123. Hatcherson J. 2019 Tourism, representation and compensation among the Dukha reindeer herders of Mongolia. *Open Agric.* **4**, 608–615. (doi:10.1515/opag-2019-0058)
124. Peemot VS. 2022 Livestock dung use in steppe pastoralism. *Siberica* **21**, 3–24. (doi:10.3167/sib.2022.210102)
125. Rasiulis N. 2016 Freestyle bearing: work, play, and synergy in the practice of everyday life among Mongolian reindeer pastoralists. [Ottawa, Canada]: Université d'Ottawa / University of Ottawa. (doi:10.20381/ruor-5535)
126. Wheeler WA. 2000 *Lords of the mongolian taiga: an ethnohistory of the dukha reindeer herders*. Bloomington: Indiana University. See <https://hdl.handle.net/2022/18631> (accessed March 2024).
127. Inamura T. 2005 The transformation of the community of Tsaatan reindeer herders in Mongolia and their relationships with the outside world. (Pastoralists and their neighbors in Asia and Africa). *Senri. Ethnol. Stud.* **69**, 123–152.
128. Moore PE, Meyer JB, Chow LS. 2017 Natural resource inventory and monitoring for Ulaan Taiga specially protected areas—an assessment of needs and opportunities in northern Mongolia. Open-File Report. US. Geological Survey 2017–1025. (doi:10.3133/ofr20171025)
129. Hadjidakis DJ, Androurakis II. 2006 Bone remodeling. *Ann. NY Acad. Sci.* **1092**, 385–396. (doi:10.1196/annals.1365.035)
130. Fahy GE, Deter C, Pitfield R, Miskiewicz JJ, Mahoney P. 2017 Bone deep: variation in stable isotope ratios and histomorphometric measurements of bone remodelling within adult humans. *J. Archaeol. Sci.* **87**, 10–16. (doi:10.1016/j.jas.2017.09.009)
131. Goldberg S, Grynepas MD, Glogauer M. 2016 Heterogeneity of osteoclast activity and bone turnover in different skeletal sites. *Arch. Oral Biol.* **71**, 134–143. (doi:10.1016/j.archoralbio.2016.06.026)
132. Keeling CD. 1979 The Suess effect: ^{13}C Carbon- ^{14}C Carbon interrelations. *Environ. Int.* **2**, 229–300. (doi:10.1016/0160-4120(79)90005-9)
133. Dombrosky J. 2020 A ~1000-year ^{13}C Suess correction model for the study of past ecosystems. *Holocene* **30**, 474–478. (doi:10.1177/0959683619887416)
134. Ambrose SH. 1990 Preparation and characterization of bone and tooth collagen for isotopic analysis. *J. Archaeol. Sci.* **17**, 431–451. (doi:10.1016/0305-4403(90)90007-r)
135. Deniro MJ, Schoeninger MJ, Hastorf CA. 1985 Effect of heating on the stable carbon and nitrogen isotope ratios of bone collagen. *J. Archaeol. Sci.* **12**, 1–7. (doi:10.1016/0305-4403(85)90011-1)
136. Hammer O, Harper DAT, Ryan PD. 2022 PAST: paleontological statistics software package for education and data analysis.
137. Heuvel CE, Zhao YM, Fisk AT. 2024 Food web structure across basins in Lake Erie, a large freshwater ecosystem. *Can. J. Fish. Aquat. Sci.* **82**. (doi:10.1139/cjfas-2024-0028)
138. Levin B, Kaya C, Komarova A, Levina M, Rozanova O, Tiunov A. 2024 Large intraspecies variation in stable isotope composition of the muscle tissues in fish of the genus cyprinion (Cyprinidae) from Middle East. *Inland Water Biol* 1146–1153. (doi:10.1134/S1995082924600443)
139. Schulting RJ, Ramsey CB, Bazaliiskii VI, Goriunova OI, Weber A. 2014 Freshwater reservoir offsets investigated through paired human-faunal ^{14}C dating and stable carbon and nitrogen isotope analysis at lake Baikal, Siberia. *Radiocarbon* **56**, 991–1008. (doi:10.2458/56.17963)

140. Pleuger-Dreibrodt S, Makarewicz C. 2020 Exploitation of marine fish by pitted Ware groups at Kainsbakke and Kirial Bro. In *The pitted ware culture on Djursland: supra-regional significance and contacts in the middle neolithic of southern scandinavia (East Jutland museum publications, Band 5)* (ed L Klassen), pp. 339–368. Aarhus, Denmark: Aarhus University Press.
141. Biggs TH, Quade J, Webb RH. 2002 $\delta^{13}\text{C}$ values of soil organic matter in semiarid grassland with mesquite (*Prosopis*) encroachment in southeastern Arizona. *Geoderma* **110**, 1. (doi:10.1016/S0016-7061(02)00227-6)
142. Wittmer HU, Sinclair ARE, McLellan BN. 2005 The role of predation in the decline and extirpation of woodland caribou. *Oecologia* **144**, 257–267. (doi:10.1007/s00442-005-0055-y)
143. Golluscio RA, Austin AT, García Martínez GC, Gonzalez-Polo M, Sala OE, Jackson RB. 2009 Sheep grazing decreases organic carbon and nitrogen pools in the Patagonian steppe: combination of direct and indirect effects. *Ecosystems* **12**, 686–697. (doi:10.1007/s10021-009-9252-6)
144. Drucker DG, Bridault A, Cupillard C. 2012 Environmental context of the Magdalenian settlement in the Jura Mountains using stable isotope tracking (^{13}C , ^{15}N , ^{34}S) of bone collagen from reindeer (*Rangifer tarandus*). *Quat. Int.* **272–273**, 322–332. (doi:10.1016/j.quaint.2012.05.040)
145. Michelsen A, Quarmby C, Sleep D, Jonasson S. 1998 Vascular plant ^{15}N natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia* **115**, 406–418. (doi:10.1007/s004420050535)
146. Nadelhoffer K, Shaver G, Fry B, Giblin A, Johnson L, McKane R. 1996 ^{15}N natural abundances and N use by tundra plants. *Oecologia* **107**, 386–394. (doi:10.1007/bf00328456)
147. Olsen KC, White CD, Longstaffe FJ, von Heyking K, McGlynn G, Grupe G, Rühli FJ. 2014 Intraskelletal isotopic compositions ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of bone collagen: nonpathological and pathological variation. *Am. J. Phys. Anthropol.* **153**, 598–604. (doi:10.1002/ajpa.22459)
148. Poupin N, Mariotti F, Huneau JF, Hermier D, Fouillet H. 2014 Natural isotopic signatures of variations in body nitrogen fluxes: a compartmental model analysis. *PLoS Comput. Biol.* **10**, e1003865. (doi:10.1371/journal.pcbi.1003865)
149. Caloin M. 2004 Modeling of lipid and protein depletion during total starvation. *Am. J. Physiol. Endocrinol. Metab.* **287**, E790–E798. (doi:10.1152/ajpendo.00414.2003)
150. Barboza PS, Parker KL. 2006 Body protein stores and isotopic indicators of N balance in female reindeer (*Rangifer tarandus*) during winter. *Physiol. Biochem. Zool.* **79**, 628–644. (doi:10.1086/502811)
151. Parker KL, Barboza PS, Stephenson TR. 2005 Protein conservation in female caribou (*Rangifer tarandus*): effects of decreasing diet quality during winter. *J. Mammal.* **86**, 610–622. (doi:10.1644/1545-1542(2005)86[610:pcifcr]2.0.co;2)
152. Golovnev AV, Kukanov D, Perevalova E. 2018 *Arctic atlas of nomadic technologies*. Saint Petersburg, Russia: Peter the Great Museum of Anthropology and Ethnography (the Kunstkamera).
153. Lukina NV. 1973 Olenevodstvo vahovskih hantov. *Iz Istor Sib* **5**, 145–169.
154. Robb GN, McDonald RA, Chamberlain DE, Bearhop S. 2008 Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Front. Ecol. Environ.* **6**, 476–484. (doi:10.1890/060152)
155. Mysterud A. 2010 Still walking on the wild side? Management actions as steps towards 'semi-domestication' of hunted ungulates. *J. Appl. Ecol.* **47**, 920–925. (doi:10.1111/j.1365-2664.2010.01836.x)
156. Felton AM, Felton A, Crooms J, Edenius L, Malmsten J, Wam HK. 2017 Interactions between ungulates, forests, and supplementary feeding: the role of nutritional balancing in determining outcomes. *Mammal Res.* **62**, 1–7. (doi:10.1007/s13364-016-0301-1)
157. Liu Z, Ji Z, Wang G, Chao T, Hou L, Wang J. 2016 Genome-wide analysis reveals signatures of selection for important traits in domestic sheep from different ecoregions. *BMC Genom.* **17**, 863. (doi:10.1186/s12864-016-3212-2)
158. Windle M, Pleuger-Dreibrodt S, Clark JK, Bayarsaikhan J, Taylor W, Piezonka H. 2025 Supplementary material from: Multispecies entanglements and stable isotope signals ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in modern reindeer-herding communities of boreal Northeast Asia. Figshare. (doi:10.6084/m9.figshare.c.7747672)