The pastoralist distinction of Central Asia: isotopic and genetic approaches to food ways, mobility, and trans-regional contact from the early Bronze Age to medieval period

Dissertation
in fulfilment of the requirements for the degree "Dr. rer. nat."
of the Faculty of Mathematics and Natural Sciences
at Kiel University

submitted by

Taylor Randolph Hermes

Kiel, 2018

First referee: Prof. Dr. Cheryl Makarewicz

Second referee: Prof. Dr. Almut Nebel

Date of the oral examination: 14.06.2018

Approved for publication: 05.03.2019

The Dean

I declare that the content and design of this doctoral dissertation is my own work, apart from the guidance of my supervisors. Neither this dissertation or similar work has been submitted to another examining body. I have prepared this dissertation according to the Rules of Good Scientific Practice of the German Research Foundation.

Herein is a cumulative dissertation comprising four papers. At the time of submission to the Faculty of Mathematics and Natural Sciences, two papers are published. The remaining two papers will be submitted for publication within one year of the oral examination.

Taylor R. Hermes

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Abstracts

Paper 1: The ancient 'Silk Roads' formed a vast network of trade and exchange that facilitated the movement of commodities and agricultural products across medieval Central Asia via settled urban communities and mobile pastoralists. Considering food consumption patterns as an expression of socio-economic interaction, we analyse human remains for carbon and nitrogen isotopes in order to establish dietary intake, then model isotopic niches to characterize dietary diversity and infer connectivity among communities of urbanites and nomadic pastoralists. The combination of low isotopic variation visible within urban groups with isotopic distinction between urban communities irrespective of local environmental conditions strongly suggests localized food production systems provided primary subsistence rather than agricultural goods exchanged along trade routes. Nomadic communities, in contrast, experienced higher dietary diversity reflecting engagements with a wide assortment of foodstuffs typical for mobile communities. These data indicate tightly bound social connectivity in urban centres pointedly funnelled local food products and homogenized dietary intake within settled communities, whereas open and opportunistic systems of food production and circulation were possible through more mobile lifeways.

Paper 2: Vertical transhumance is a crucial mobility strategy for pastoralists living in montane environments. Moves to high elevations in early summer followed by descents to lower elevations in autumn allow herders to provide livestock with rich fodder resources that fluoresce at different times along orographic gradients. Archaeologically, however, isolating vertical mobility has remained challenging. In this paper, we explore the potential of using $\delta^{18}O$ time series sampled from livestock tooth enamel, which archives seasonal records of the oxygen isotopic composition of imbibed water, to detect vertical transhumance. Marked distinctions in the $\delta^{18}O$ values of meteoric waters between low and high elevations provide a strong basis for observing isotopic signals in livestock teeth that are consistent with vertical mobility. Using $\delta^{18}O$ values of precipitation measured from lowland and highland sites in the Alps, we detail a conceptual model for detecting vertical transhumance that is applicable in montane environments around the world. We further discuss the limitations of our approach and improvements to be explored with future research.

Paper 3: The dispersal of millet agriculture out of northern China in the early Bronze Age (third millennium BC) marked a pivotal development in transcontinental exchanges of domesticated plants and animals. After a long delay since domestication in the early Holocene, broomcorn millet was present in the steppe margins of eastern Kazakhstan by circa 2300 calibrated years (cal) BC, but a paucity of archaeobotanical evidence and also human remains for stable isotope analysis to measure dietary intake precludes resolving millet cultivation or its importance in human diets amid this initial crop translocation. However, livestock skeletal remains recovered from settlement sites of nomadic pastoralists are abundant. We report that by the first half of the third millennium cal BC pastoralists in the Inner Asian Mountain Corridor cultivated millet at scales large enough to provision their herds of sheep, goat, and cattle with agricultural byproduct. Stable isotope analysis of livestock teeth reveals cycles of winter foddering with millet, and analysis of bone collagen demonstrates that foddering persisted over animal lifetimes. Intensive livestock foddering by pastoralists indicates that precocious cultivation coincided with the spread of millet into the steppe zone, implying that pastoralists had existing farming proficiency with Near Eastern domesticates.

Paper 4: Goats (*Capra hircus*) were domesticated in the Near East about 11,000 years ago and spread across Eurasia as an economically productive and environmentally resilient herd animal. While the geographic origins of domesticated goat lineages are well established, the pathways taken by pastoralists and agriculturalists that translocated goats across Asia during the early Bronze Age (ca. 3000-2000 cal BC) and later periods remain unclear. In this paper, we analyze the sequences of hypervariable region I and cytochrome *b* in the mitochondrial genome of Bronze and Iron Age goats from archaeological sites located along proposed translocation vectors into Central Asia. Since the late Bronze Age (ca. 1600-1000 cal BC), high genetic diversity was present in the Tian Shan and Dzhungar ranges of the Inner Asian Mountain Corridor, indicated by mtDNA haplotypes representing lineages A and C, in addition to the very rare D lineage. In contrast, only mtDNA haplotypes of lineage A were observed in the northerly "Eurasian steppe belt." These findings suggest that early herding communities living in montane ecosystems were drawing from genetically diverse goat populations, likely via the Iranian Plateau, while northern steppe communities had goats reflecting a founder population, possibly via eastern Europe.

Kurzfassungen

Paper 1: Die historische Seidenstraße bildete ein weitreichendes Austausch- und Handelsnetzwerk, das den Transport von Gütern und landwirtschaftlichen Produkten durch ganz Zentralasien sowohl über sesshafte, urbane Gesellschaften als auch über mobile Viehhirten ermöglichte. Auf der Grundlage einer Untersuchung von Ernährungsmustern als Ausdruck sozioökonomischer Interaktion haben wir Kohlenstoff- und Stickstoffisotopen an menschlichen Überresten analysiert, um den Nahrungsverbrauch in sesshaften urbanen und in hirten-nomadischen Gesellschaften zu erfassen, und darüber isotopische Nischen modelliert. Dies ermöglichte uns, die Nahrungsdiversität und Vernetzung dieser Gruppen zu charakterisieren. Die gefundene geringe isotopische Variabilität innerhalb urbaner Gruppen bei gleichzeitiger isotopischer Abgrenzung zwischen verschiedenen urbanen Gemeinschaften unabhängig von lokalen Umweltbedingungen deutet darauf hin, dass auf lokaler Ebene primär Subsistenzwirtschaft zur Nahrungsproduktion betrieben wurde anstatt landwirtschaftliche Güter über externe Handelsrouten zu beziehen. Nomadische Gemeinschaften zeigten dagegen ein hohes Maß an Ernährungssdiversität, das auf ein breites Spektrum an Nahrungsmitteln hindeutet, welches typisch für mobile Gemeinschaften ist. Die Ergebnisse der Studie zeigen, dass sich urbane Zentren über eng gewobene soziale Netzwerke gezielt mit lokal produzierten Lebensmitteln versorgten, was sich in einer homogenen Ernährung widerspiegelt, während mobile Lebensweisen eine offene und breit angelegte Nahrungsproduktion und weitergabe ermöglichten.

Paper 2: Vertikale Transhumanz (Wanderweidewirtschaft im Gebirge) ist eine wichtige Wirtschaftsstrategie von mobilen Viehhirten, die in Gebirgslandschaften leben. Der Aufstieg auf Hochebenen im Frühsommer gefolgt vom Abstieg in Tiefebenen im Herbst erlaubt Viehhirten, ihre Herden mit möglichst reichhaltigen Futterressourcen zu versorgen, die in unterschiedlichen orographischen Höhen verfügbar sind. Archäologisch ist es allerdings nach wie vor schwierig, diese vertikale Mobilität zu erfassen. In diesem Artikel untersuchen wir den potentiellen Nutzen von δ^{18} O-Zeitreihen, um vertikale Transhumanz zu erfassen. Die Datenpunkte basieren auf einer seriellen Zahnschmelz-Beprobung von Nutztieren die eine saisonale Abfolge der isotopischen Sauerstoffzusammensetzung des aufgenommenen Wassers widerspiegeln. Deutliche Unterschiede in den δ¹⁸O Werten meteorischen Wassers zwischen unterschiedlichen Geländehöhen bieten eine fundierte Grundlage für die Untersuchung von Isotopensignalen in Nutztierzähnen, die mit vertikaler Mobilität einhergehen. An Niederschlagswasser in Niederungen und Hochebenen der Alpen gemessene δ^{18} O Werte erlauben die Erstellung eines Modells für die Erkennung vertikaler Transhumanz, welches in Gebirgslandschaften auf der ganzen Welt anwendbar ist. Darüber hinaus diskutieren wir die Grenzen unseres Forschungsansatzes und mögliche Verbesserungen durch zukünftige Forschung.

Paper 3: Die Ausbreitung des Hirseanbaus aus Nordchina in der Frühbronzezeit (3. Jahrtausend BC) kennzeichnet eine grundlegende Entwicklung transkontinentalen Austausches domestizierter Pflanzen und Tiere. Lange nach seiner Domestikation im Frühholozän tritt die Rispenhirse erstmalig um circa 2300 cal BC an den Rändern der Steppe Ostkasachstans auf. Der Mangel an archäobotanischen Daten und menschlichen Überresten für die Analyse stabiler Isotopen zur Untersuchung von Ernährungsmustern erschwert die Entschlüsselung der initialen Translokation der Rispenhirse als Anbaugetreide und seiner Bedeutung als menschliches Nahrungsmittel. Im Gegensatz dazu sind Knochenfunde von Nutztieren aus Siedlungsplätzen nomadischer Viehhirten häufig. Mit der vorliegenden Studie konnte gezeigt werden, dass Viehhirten innerhalb der innerasiatischen Gebirgsschneise ab der ersten Hälfte des 3. Jahrtausends cal BC Hirse in einem Ausmaß anbauten, das ausreichte, um ihre Schaf-, Ziegen- und Rinderherden mit landwirtschaftlichen Nebenprodukten dieser Nutzpflanze zu versorgen. Die Analyse stabiler Isotopen an Nutztierzähnen sowie an Kollagen aus Knochen zeigte die zyklische Winterfütterung mit Hirse und, dass diese Zufütterung über die gesamte Lebenszeit der Tiere geschah. Die intensive Fütterung von Nutztieren durch Viehhirten impliziert, dass früher Pflanzenanbau zeitlich mit der Ausbreitung der Hirse in der Steppenzone zusammenfällt. Dies deutet darauf hin, dass diese frühen Viehhirten bereits Erfahrung mit dem Anbau domestizierter Pflanzen aus dem Nahen Osten hatten.

Paper 4: Ziegen (Capra hircus) wurden im Nahen Osten vor ungefähr 11.000 Jahren domestiziert und breiteten sich als wirtschaftlich ertragreiche und ökologisch widerstandsfähige Nutztiere über Eurasien aus. Während die geographischen Ursprünge der Abstammungslinien domestizierter Ziegen gut belegt sind, sind die Wege, auf denen Ziegen durch Viehhirten und Ackerbauern in der frühen Bronzezeit (ca. 3000 bis 2000 cal BC) und später nach Asien verbreitet wurden, nach wie vor unklar. In diesem Artikel analysieren wir die hypervariable Region I und Cytochrom b in der mitochondrialen DNA bronze- und eisenzeitlicher Ziegen aus archäologischen Fundorten

entlang bestimmter Translokationsvektoren nach Zentralasien hinein. Ein hohes Maß genetischer Diversität war bereits seit der späten Bronzezeit (ca. 1600 bis 1000 cal BC) in den Gebirgsketten Tian Shan und Dzhungar um die innerasiatische Gebirgskette vorhanden, was durch mtDNA-Haplotypen angezeigt wird, die die Abstammungslinien A und C sowie die seltene Abstammungslinie D repräsentieren. Im Gegensatz dazu wurden im nördlichen "Eurasischen Steppengürtel" nur mtDNA-Haplotypen der Abstammungslinie A beobachtet. Die Ergebnisse dieser Studie legen nahe, dass die frühen in Bergregionen lebenden viehhaltenden Gemeinschaften Ziegen aus genetisch diversen Populationen bezogen, wahrscheinlich über das Iranische Hochland. Demgegenüber hielten nördlichere Steppengemeinschaften Ziegen aus einer Gründerpopulation mit vermutlich osteuropäischem Ursprung.

Acknowledgments

It would be unjust to limit my words of gratitude only to individuals who played a role in the development of this work since I began my PhD research at Kiel University in November 2014. Numerous people had a profound impact on me that ultimately made the completion of this dissertation a reality.

I'll begin by thanking my parents, Kim and Randy, and my brother Collin. They have been the core of my support network with unwavering help and outside perspectives at every twist, turn, high, and low of my academic career. I could not have done it without you.

As an undergraduate student at Washington University in St. Louis, I initially decided to study biochemistry but ultimately settled on anthropology. I'll never forget the words of encouragement that my biochemistry major advisor, T.J. Kappock, gave me in the moment I broke the news: "You're not the type of person who should spend his time underground in a chemistry lab."

Through (mis)adventures with my dear college friends, Kevin Croker, Alan Pappalardo, Justin Strohm, Nick Apperson, and John Klacsmann, we strengthened one another, whether jamming in the radio station, thrashing hills on longboards, or cultivating grand ideas for the future, many of which have materialized for each of us. Thank you, and Godspeed!

Upon my switch to studying anthropology, I met a new assistant professor teaching a class I enrolled in by chance, "From Rock and Roll to Heavy Metal: Ancient Civilizations of the Old World." After a couple weeks into the class, I decided I should embark specifically upon archaeology. My interest caught the eye of the professor, Michael Frachetti. I'll be honest: when he invited me to his excavations in Kazakhstan, I had no idea it was a real country. He showed me how to apply for research grants and how to engage with the study of the past. Michael has been a key figure in the growth of my work, and I hold him close to my heart. My first time on his excavation in 2006, I met Paula Doumani, Marc Meyer, Lynne Rouse, and Juli Huang who would turn out to be solid friends and colleagues in the years that followed. This first experience of doing archaeology with that cast of characters sealed the deal. Thank you!

I am deeply thankful for Lois Beck, who helped me craft my fledging ideas about culture and nomadic pastoralists through intensive writing courses and long discussions over Persian food. I am forever indebted to her kindness and wisdom she shared with me. In the days leading up to graduation from Washington University, I remember fondly having dinner and drinks with Lord Colin Renfrew, who passionately talked to me about my newfound ideas on the Bronze Age in Central Asia. Most importantly he listened to my stories of music, social gatherings, and many other topics that had nothing to do with archaeology. Though over 10 years ago, these experiences in St. Louis are still very much so alive in my memory and have directly informed the academic foundation that this dissertation is built upon.

At the University of Arizona, I was fortunate to be a part of a close-knit archaeology cohort. Thank you, Jessica MacLellan, Saul Hedquist, Lewis Bork, and Ben Curry for workshopping ideas, commenting on papers, and having fun with me in the desert. My friends in other cohorts and sub-disciplines of anthropology were instrumental in shaping my thoughts about the study of the past and present. Thank you, Amy Clark, Matthew Pailes, Shane Miller, Randy Haas, Marijke Stoll, Sam Fladd, Mary Good, and those mentioned above for the hours upon hours of discussion, sharing nachos, and enjoying beers ranging from Gentle Ben's to the stuff for pretentious hipsters. There are faculty members at the School of Anthropology whom I particularly want to offer heartfelt thanks: David Killick, Lars Fogelin, Michael Schiffer, and Stephen Lansing. I have special words for the late Bill Longacre, who took me in as his final mentee. He shared his humor, compassion, and intellect with me. I wrote my first academic

publication with Bill, and I will forever cherish the memories of him. I learned a tremendous amount from these giants and each provided profound support during dark days. There is an unusual acknowledgement that I must give to John Olsen, Mary Stiner, and Mark Aldenderfer who unwittingly provided me with an extraordinary opportunity for career advancement that set in motion a cascade of events leading me to Kiel. Thank you.

I only recently learned that my most dependable SAA conference pal, Josh Wright, had worked behind the scenes to prop me up on the radar of my current supervisor, Cheryl Makarewicz. In writing this now, I feel a swell of emotion because I am utterly beholden to his grace. Thank you, Josh.

Truly, I would be nowhere without the guidance of my primary supervisor, Cheryl. I've told her once before that she saved my life. This is not an exaggeration. Cheryl brought me in and built me up. It has been a massive pleasure to work closely with her over the past three years, and I look forward to our future research together. Equally, I have an immense amount of gratitude for my secondary supervisor, Almut Nebel, who gave me special opportunities to do ancient DNA research as an outsider to biomolecular work. Thank you, Almut. My journey has come almost full circle via the aDNA lab. I cannot begin to describe the overwhelming sense of déjà vu I experienced when I began pipetting my first PCR master mix in Kiel, echoing my undergraduate days in the biochemistry lab.

Indeed, I spent a considerable amount of time in the aDNA lab and stable isotope lab in order to gather the data for this dissertation, and there are many to acknowledge who showed me the tricks of the trade. I especially thank Lisa Böhme who helped me launch the research reported in Paper 4. Lisa, you are a dear person to me, and our friendships transcends all present and future plights. Big thanks are due to Alex Flasche and Kim Callan who helped with lab work when I was busy rinsing enamel and collagen samples in the isotope lab. The skills I developed to precisely sample enamel from livestock teeth can be traced back to Johannes Hänel, who showed me the work flow of drilling teeth with a Dremel. I also want to thank Sarah Pederzani for rich discussions about stable isotopes and data analysis. Thank you to Sarah Pleuger who kindly provided the German translations of the abstracts for each paper in this dissertation. I eagerly look forward to working with her in the following years. I also want to thank Fabian Haase and Sven Gauter for often watching my high-maintenance dog, Buddha, while I worked in the isotope lab, in addition for generally being outstanding friends.

The vast majority of the archaeological materials behind the data in this dissertation reflect two decades of collaboration between Alexei Mar'yashev of the Institute of Archaeology in Almaty, Kazakhstan and Michael Frachetti. Although I began working on their project in 2006 and became a co-director of it in 2012, the groundwork for the excavations and scientific design could would not have been possible without Alexei, who tirelessly dedicated his career to the study of Bronze Age communities in eastern Kazakhstan. In March 2018, we learned that Alexei passed away at 85. He continued to climb mountains and go on expeditions until the very end. He was a great archaeologist, storyteller, athlete, and comedian. Rest in peace.

During my time working in Kazakhstan and Uzbekistan, numerous people have helped organize, facilitate, and support the logistics of my research and that of our wider team. Thank you to Farhod Maksudov, Olga Gumorva, Yuri Peshkov, Dimitry Voyakin, Ekaterina Dubagina, Roman Ilin, Egor Kitov, and Volodiya Strizhenkov. These individuals come from various background in and outside of academia, but they all share warm hearts, strong work ethic, and firm commitment to each and every mission we embarked on together.

As my research has picked up pace in the last three years, I am enormously thankful for the friendships and scientific partnerships of Robert Spengler, Elissa Bullion, Yuqi Li, Giedre

Motuzaite-Matuzeviciute, and Miljana Radivojevic. We have numerous ongoing collaborative projects that will result in new discoveries and good fun in the years ahead.

Finally, and most importantly, I thank my wife, Britt Marie. With her love and encouragement, she enabled me to succeed. She helped at each stage of my research, whether helping me process samples in the lab to proofing text. I love you. This body of work is dedicated to you and our daughter to be.

To all, here you go.

Introduction

Central Asia has been an important crossroads between settled agriculturalists and pastoralist communities since at least the third millennium BC¹⁻³. Numerous cultural and historical phenomena emerged in the vast grasslands of the Eurasian steppe zone that helped shape the social and institutional developments of the Old World. Indeed, these events and processes stretch back in time to the initial dispersals of hominins into Inner Asia and complex admixtures between archaic humans. Neanderthals, and Denisovans during the Pleistocene^{4,5}. It was not until the mid-Holocene when the long trajectory of hunter-gatherer society began a transformation into fully-fledged food production based on herding domesticated herbivores⁶. During this process, trans-regional exchanges accelerated which contributed to the movement of people from the far corners of the steppe zone⁷⁻⁹, the spread of Indo-European languages across the region and into south and east Asia^{7,10,11}, the rise of bronze technology^{12,13}, the proliferation of riding domesticated horses^{14–16}, and the transfer of domesticated plants and animals from homelands of domestication that were external to the steppe zone¹⁷⁻¹⁹, all of which had profound impact on local and regional cultural processes for pastoralist and settled communities alike. By the historical period, Central Asia had evolved into a region of highly dynamic levels of interaction between Europe, the Near East, and east Asia that is commonly referred to as the "Silk Roads"²⁰. During this time, Central Asia became the dominion of powerful steppe empires that supposedly rattled settled folk for centuries²¹. While Central Asia is a vital region for studying important human developments, archaeological research in the region is still sparse, and this is especially the case in applying scientific methods to study the intersection of biology, culture, and ecology in this significant section of the world.

In this cumulative dissertation, I offer four case studies, presented here as Papers 1-4, concerning the distinction of human lifeways that are focused on the management of herd animals, typically, sheep, goat, cattle, horses, and camels (but also in other regions of the world, reindeer, yak, and camelids)²². These so-called "nomadic" lifeways are in contrast to living in singular places, typically urban spaces and large settlements, that echo familiar human experiences to what we know from the modern world²³. The fundamental distinction of pastoralist societies, compared to settled communities, is a huge degree of subsistence adaptability, which depends on knowledge and practice of enhancing the human-animal relationship. Unlike in settled agricultural societies, it is useful to consider that flexibility is deep-seated in pastoralist societies, emphasizing a high capacity to be mobile, maintain cultural order, and produce food. As the papers in this dissertation use various terms to describe pastoralists while advancing a new scientific understandings of food production, mobility, and cultural interaction over great distances by people who orient their lifeways near animals, it is important to examine cultural categories critically prior to breaking into the research studies in this dissertation, as there are abundant classifications for pastoralists.

The pastoralist typological trap

Pastoralists are often confused with nomads, and in some academic circles, choosing one term over the other can raise objections. The terms "nomadism" and "pastoralism" suggest the rearing of livestock²⁴, but scholars typically associate "nomadism" as a mobility strategy, which can also characterize hunter-gatherers, while "pastoralism" is a strategy of food production based on domesticated herbivores²⁵. Historians commonly conceive "nomads" to represent the horse-riding peoples that were described in ancient texts in classical civilizations from Greece to China^{21,26–28}. Among archaeologists, "nomadic" generally reflects movement and food production primarily based on animal husbandry^{29–31}. Encoded in pastoralist subsistence, there is the specific practice of herding, which Humphery and Sneath define as having a "personal presence with livestock on the

pastures"³². Indeed, this definition highlights the human-animal relationship as a central feature of pastoralist food production, serving as the focal point for knowledge transmission, group identity, and livelihood. Scaling up from this practice, the ability for people to organize society around animal management readily emerges, of which divergent and interweaving trajectories of cultural expression and complexity are vibrant^{33–37}.

Perhaps the most prolific proponent, and most cited, of pastoralist typologies is Anatoly Khazanov, who categorizes pastoralists into five types: 1) pure pastoral nomadism, 2) seminomadic pastoralism, 3) semi-sedentary nomadism, 4) distant-pastures husbandry, and 5) seasonal transhumance²². While Khazanov's typologies have dominated the research framework for pastoralist societies, it should be recognized that his divisions do not deal well with reconciling social or political transformations among pastoralists nor do they effectively capture the inherent variability of pastoralist societies. His definitions boil down to a society's extent of migratory mobility, the primacy of specific animals in producing subsistence products, and the degree of symbiosis between nomadic and settled agricultural communities. In general, historians from Russian academic traditions, rather than anthropologists, have generated the vast amount of literature on Eurasian pastoralists³⁸. which over emphasize linear evolutionary trajectories of cultural development, often directly inspired from Marxist theories that were commonly applied during the Soviet period³⁹. Such evolutionary models, when used to analyze cultural phenomena, always suffer from an inability to deal well with hybrid forms or explain change from one mode to another⁴⁰. Anthropologists recognize that categorical designations of pastoralists, or any society for that matter, do not encapsulate discrete packages of cultural traits. Cultural variation and change are constant social outcomes of internal and external forces, many of which cross-cut multiple domains of classification commonly used by social scientists, such as culture, ecology, politics, and economy^{41,42}.

Pastoralist strategies reflect degrees of adaptation to an ever-present dynamic of social, political, and environmental conditions^{29,33,34,43}. Archaeologically, however, engaging with the fine-grained information present in the ethnographic record does not immediately offer clear paths towards understanding ancient society⁴⁴. There are stumbling blocks in using analogies from the present to characterize the past—a pattern that has long been an affliction of archaeological studies in Central Asia⁴⁵. Perhaps one of the most salient ethnographic examples that is instructive of this "pastoralist problem" is the story of the Kyrgyz in the Wakhan Corridor of Afghanistan and their dramatic shifts in mobility patterns during the 20th century.

Before the end of World War II, the Kyrgyz employed patterns of long-distance seasonal migrations to provide graze for their livestock and to access markets for trade by annually moving up to 150 km to interact with agriculturalists settled in low elevation valleys in China, Tajikistan, and Afghanistan⁴⁶. Mobility patterns and associated social interactions with neighboring populations were then drastically affected by changes in the political geography of China and the USSR in the late 20th century, resulting in the entire community of several thousand being confined to a sort of "no-man's land" in the Wakhan Corridor, a narrow valley in the pan-handle of Afghanistan ranging between 3,000 and 5,000 m.a.s.l. on the valley floor⁴⁶. Since the community was cut-off from the outside world, their pattern of movements became shorter and more frequent in this extreme environment, but despite changes in their overarching ecological setting, the Kyrgyz reshaped their food production strategies and maintained strong group identity⁴⁶.

The case of the Kyrgyz's shifting patterns of mobility and cultural adaptation further emphasize how essential typologies of pastoralists fail, while highlighting the flexibility of pastoralist lifeways. First, the Kyrgyz's adaptation to a particular alpine ecological zone altered their patterns of movement, and this situation can be documented ethnographically

in detail, as Shahrani cogently describes⁴⁶. It is not entirely clear which of Khazanov's types of pastoralism applies for the former or latter condition of the Kyrgyz. One could argue the community went from being "semi-nomadic" to practicing "distant-pastures" pastoralism. Their prior patterns of mobility involved moving through a sequence of locales to access pastures, while the latter involved more fixed residence with smaller groups moving herds to pastures seasonally, but then returning to home bases, similar to logistical foraging of hunter-gatherers⁴⁷. Secondly, while ethnography provides details of the different strategies of the Kyrgyz before World War II and the Kyrgyz after their isolation, which can be traced directly to geopolitics⁴⁶, the mobility patterns of the community members characterize a long-term cultural arc, following changes in social dynamics and their environmental setting. From an archaeological perspective, the isolation of the Kyrgyz is a small blip on the radar of long-term process. That is, the strategies adopted by the Kyrgyz reflect a larger pattern of variation.

The case of the Kyrgyz of the Wakhan Corridor is useful in demonstrating the adaptive response of pastoralist communities to external forces while also illustrating how these processes can be conceptualized from opposing points of view. Most importantly, this example exposes the shortcoming of typologies that characterize communities as being fixed in time. For this dissertation, I argue that types of pastoralism are not analytically useful, and I adopt a more pragmatic approach by assuming a great deal of flexibility in lifeways that are oriented around human-animal relationships, which are shaped to local circumstances. I use the terms pastoralism, nomadism, herding, animal husbandry, and livestock management pragmatically for particular cultural contexts. In doing so, I implicitly follow Spooner's "generative model of nomadism". whereby, particular sets of data directly inform aspects of culture and social organization without rigid behavioral classes. This approach enables a less biased framework for studying pastoralist society, since practices such as mobility, plant cultivation, and social interaction, can be operationalized with data and analyzed outside of close-looped typologies.

Recent archaeological research across the steppe zone has broadly adopted this general format in dealing with the theoretical linkages between archaeological data and ancient society. It is now widely recognized that pastoralists are highly adaptable and that patterns of variability can be recovered from the archaeological record⁴⁸. This is a departure from traditional conceptual frameworks for identifying pastoralists in the archaeological record by examining a limited number of data classes, such as the ephemeral nature of pastoralist encampments, prevalence of livestock skeletal remains, or settlement patterns in so-called marginal areas 30,49. A common problem here is that comparisons were typically made in reference to settled communities, echoing a history of science that viewed the emergence of the first pastoralist societies in the Near East as being dependent on proto-urban centers⁵⁰. Now, scholars approach material evidence of pastoralism with a strong interest in studying nuance and protracted processes that are intimately tied to local context, while also representing these communities under study in their own right^{45,51–53}. Field research in Central Asia over the past decade has resulted in a paradigm shift in learning how pastoral societies can drive far-flung cultural processes and initiate profound social changes^{54–57}. It is on this conceptual wave of advance that the theoretical orientation of this dissertation is placed. Crucially, the isotopic and genetic approaches applied in this dissertation attempt to provide a basis to recover evidence of both fine-grained and wide-scale pastoralist behavior. Again, the case of the Kyrgyz and the shortcomings of typological approaches demonstrate the need to examine multi-scalar evidence for the study of pastoralists.

"Pastoralism" in the papers herein

In the papers of this dissertation, particular instances arise that directly confront traditional understandings of pastoralists, while others play into the hands of conventional concepts where appropriate. Since these are not pointed out explicitly in each paper, due to length requirements in preparing manuscripts for publication, I'll offer examples for each.

In the first paper, "Urban and nomadic isotopic niches reveal dietary connectivities along Central Asia's Silk Roads," the potentially problematic term "nomadic" comes up immediately. Here, this term is wielded in order to contrast more mobile ways of life during the medieval period (2nd to 16th c. AD) with life that was anchored to large urban centers. During the Silk Roads period in Central Asia, there is little doubt surrounding the political and economic influence of large population centers. However, there is also an apparent tension in the historical record concerning nomadic communities that are often lumped together and dubbed "Turkic tribes" 58. This study examines the dietary diversity of communities that comprised Silk Road phenomena by analyzing variability in carbon and nitrogen stable isotope ratios (δ^{13} C and δ^{15} N) in human bone collagen as a means to access cultural distinctions that are not recorded in historical texts. The isotopic composition of bone collagen archives 10-15 year dietary averages⁵⁹, which allows for individual subsistence histories to be characterized. Ahead of the analysis, cultural classifications were not strictly assigned, which allowed the isotopic patterns to help drive how communities should be grouped. Simply put, "nomadic" or "urban" types were generated out of the data themselves, in accordance with the approach offered by Spooner³⁸. In particular, I settled on "nomadic" to better interface with a large body of historical work that relies on this term to describe the Turkic populations supposedly riding on horseback and generally documented as being antagonists to settled lifeways^{21,26}. Indeed, I do not reinforce this conception but instead directly challenge it. The nomadic communities we analyzed exhibited much wider ranges of isotopic variability, which is indicative of highly diverse diets among individuals. This finding suggests that so-called nomadic groups may have been strong influencers of food culture along the Silk Roads, thus relegating urban contexts to a restricted sense of food drudgery that is not well reflected in historical texts.

In the second paper, "Ahead of the curve? Implications for isolating vertical transhumance in seasonal montane environments using sequential oxygen isotope analyses of tooth enamel," we deal with a specific type of mobility strategy that pastoralists employ, in which they migrate to the mountains in the summer months to provide livestock with rich pastures growing at different times depending on elevation. Archaeologists have long assumed that ancient Eurasian pastoralists employed this approach based on finding settlement sites at the base of mountains which are exploited today by herding communities^{45,60}. This almost one-to-one analogy between the past and the present is a reasonable place to begin scientific inquiry, but it cannot provide direct evidence for vertical movements with animals. Here, I thought it would be useful to conceptually frame what vertical transhumance would look like in the oxygen isotopic composition (δ^{18} O) of tooth enamel of an animal that moved from low to high elevation and back. Livestock teeth incrementally archive isotopic inputs that can be isolated as time series by sequentially sampling enamel along the tooth growth axis. (This method is also central to Paper 3.) The oxygen isotopic composition of enamel is directly related to that of imbibed waters^{61,62}, which are governed by the seasonality of the hydrological cycle in any given location⁶³, but is further modified by orographic effects of landforms, which we exploited in this paper⁶⁴. We found a high potential for isolating vertical moves by livestock by measuring δ^{18} O values in tooth enamel that reflect the oxygen isotopic composition of meteoric waters between low and high elevation. In this paper, we directly engage with vertical transhumance, which is but one type of mobility that pastoralists can apply in Central Asia. We aimed to formulate a means to measure the

intensity of movement, which more generally can provide an estimate of ancient pastoralist behavioral variability.

In the third paper, "Millet farming by early Bronze Age herders coincided with first crop transmissions across Eurasia," we describe the initial adoption of a new cereal crop, which was domesticated in northern China, by pastoralist communities in the Eurasian steppe zone. It is in this paper where fundamental questions about who a pastoralist is and who an agriculturalist is come into play. Using a stable isotopic analysis of δ^{13} C and δ^{18} O values sampled from livestock tooth enamel and also δ^{13} C and δ^{15} N sampled from livestock bone collagen, we effectively show that the earliest millet farming in this vast region was likely motivated by provisioning domesticated animals with agricultural by-products at high intensity since ca. 2800 cal BC. People were winter foddering animals with millet, which is readily detectable in the carbon isotopic composition of skeletal remains, on account of millet (C_4 plant) imparting high δ^{13} C values in consumer tissues⁶⁵, relative to the C_3 dominant steppe zone that imparts low δ^{13} C values in people and animals. Here, we take a wide definition of pastoralism that absolutely includes the ability for such communities to engage in intensive plant cultivation. Using the pastoralist designation here is especially relevant because farming activities appear to have been directed towards animal husbandry as a possible reason for adopting a new crop. This study further implies that Inner Asian pastoralists had existing knowledge of wheat and barley farming, which easily enabled them to incorporate millet cultivation into existing practices. This research is arguably the core of this dissertation, and ushers in a completely new understanding of the synergy between plant cultivation, herding, and trans-regional cultural contacts at a critical moment in Eurasian prehistory. This is a clear-cut example of multi-resource pastoralism that continued up into the historical era as demonstrated by Paper 1⁶⁶.

In the final paper, "Mitochondrial diversity of ancient goats in Eurasia and translocation vectors of pastoralist economies into Central Asia," I shift from a stable isotopic approach to a genetic analysis of domesticated and wild goats from Bronze and Iron Age sites across Central Asia. While ancient DNA studies are being rapidly executed on human remains from across Eurasia by a small number of labs⁷⁻⁹, investigations of ancient animal genetics have lagged behind⁶⁷, despite these biological systems serving a central role in the cultural activity of communities across the wider region. Since goats were domesticated in the Near East by 8,000 cal BC and spread across Eurasia throughout the mid-Holocene, we attempted to track inter-regional intensities of gene flow as a measure of social connectivity. We found that Bronze Age goats from the Inner Asian Mountain Corridor, which is a series of foothill ecologies that latitudinally spans Inner Asia from the Pamir to Altai Mountains, contained greater mitochondrial diversity expressed in the hypervariable region I. In contrast, goats from the Eurasian steppe belt, which is a flat grassland ecozone spanning the length of southern Russia and northern Kazakhstan, were characterized by less diversity. This suggests that the mountain zones were important loci for cultural interaction and the exchange of livestock. The findings imply that regionally defined genetic spheres might be further uncovered in order to infer the geography of social connectivity that studying human genetics cannot easy access due to a paucity of samples. In this paper, pastoralism is simply used to convey an understanding that people formed close relationships with animals which modified their genetic composition, likely through a complex mixture of migration, selective breeding, and social interactions in the unique grassland environments of Central Asia.

Central Asian Environments in the Eurasian steppe zone

The Eurasian steppe zone is a vast ecological band that extends from the western shores of the Black Sea to the eastern end of Mongolia and is situated between the forests at about 57° N latitude and the deserts of Uzbekistan, southern Kazakhstan, and northern China (Fig. 1). While broadly defined, the steppe zone is further divided into five major land-cover classes that reflect variation in continental climate according to latitude: 1) forest steppe, 2) steppe, 3) semi-arid steppe, 4) arid steppe, and 5) mountain steppe⁶⁸. These ecological zones represent a gradient from north to south of decreasing precipitation, increasing summer temperatures, and more growing-degree days⁶⁸. This gradient is less relevant for the mountain steppe, which is characterized by botanical variation driven by elevation. A key geographical feature discussed in this dissertation is the Inner Asian Mountain Corridor (mentioned above) that facilitated inter-regional biological exchanges and cultural contact^{17,69}.



Fig. 1. The extent of the Eurasian steppe zone (light blue) according to ecological definitions for continental grasslands. (Image source: Wikimedia Commons.)

The intense seasonality of steppe environments is significant for how pastoralists exploit grassland pastures for their livestock. The distribution of steppe grasses varies not only latitudinally between arid steppe, semi-arid steppe, steppe, and forest steppe, but also by elevation in mountain steppe regions. In general, in semi-arid steppe zones, the growing periods for the dominant vegetation (*Stipa*, *Carex*, and *Artemisia*) occur at different times relative to one another but, together, create sequences of blooming patterns in close succession. These botanical rhythms are crucial for pastoralists in providing graze to their livestock by shaping mobility patterns accordingly. While over relatively low elevations in the open steppes of central Kazakhstan, for example, movements following seasonal botanical growth have been documented to span great distances, on the order of 100 to 200 km, but in some cases over 500 km annually^{70,71}. However, in the Inner Asian Mountain Corridor the distances needed to travel through these seasonal botanical cohorts are significantly shorter, perhaps spanning no more than 10 km⁴⁵.

Shorter seasonal migrations in mountain regions have the potential to bring groups together into highly predictable and productive pastures that are accessible through branching river valleys and high-elevation passes. Recent research has used computer simulations to model the pathways formed by these seasonal mobility patterns in Central Asia's mountains found that up to 70% of known Silk Road sites were located along these routes⁷². This is a major

finding owing to the fact that the highland Silk Road routes emerge from nomadic ecology rather than using the locations of sites in the model a priori. For pastoralists, the mountain steppe is an environmental niche that likely had significant social and political implications, where resources are rich, but space is limited, thus serving as a constant socioenvironmental engine that drives interaction—a central theme of the papers in this dissertation.

Isotopic and genetic approaches

While the papers in this dissertation are self-contained studies, a few words to describe the overall approach of my doctoral research are in order. The papers herein exploit biological systems to study ancient pastoralists, especially their engagements with steppe grassland environments and one another, which in most cases have profound scaling up effects that facilitated trans-continental cultural phenomena.

Stable isotope analysis has been applied to study archaeological problems in Central Asia with increasing frequency^{73–85}. However, the first three papers introduce analytical techniques that are new to archaeology. In Paper 1, we operationalize the concept of the isotopic niche in order to study human dietary diversity. An isotopic niche reflects the resource exploitation in the ecological niche of a community of organisms and serves as a direct measure of inter-individual dietary behavior^{86,87}. This study was the first to apply this framework in human communities, whereas previously the tool has been used to study animal ecology^{88–90}. Paper 1 demonstrates the utility of analyzing isotopic niches between communities that are differentiated based on settlement systems, which were parsed by classifications of "nomadic" vs. "urban."

Paper 2 applies a subtler methodological advance by presenting a conceptual model of how vertical transhumance would be expressed in isotopic time series of tooth enamel of mobile livestock. Previous research has established models for dietary shifts in livestock and have tested these against controlled feeding studies⁹¹, but this paper was the first to setup a heuristic framework for how environmental inputs can be used to measure vertical mobility as an independent system. Since the publishing of this paper, a study by Makarewicz provided a solid demonstration of resolving vertical mobility by comparing the oxygen isotopic variability in tooth enamel between domesticated cattle and sheep to wild gazelle⁹². This is an important advance, and Paper 2 will serve as a foundation to execute a case-controlled study with modern animals to test the models presented with respect to Makarewicz's method.

Paper 3 offers a new empirical basis to understand the practice of millet agriculture by pastoralists through an intensive examination of livestock isotopic ratios that is then used to generate seasonal models of dietary intake. To the best of my knowledge, this study is the first of its kind to generate unified annual cycles of isotopic time series sampled from livestock teeth, which here, provides an easy-to-read graphical representation of winter foddering with millet. Furthermore, these data were fed into a stable isotopic mixing model that provided estimates of the relative proportions of millet by-product and C₃ vegetation in livestock diets. This model and the isotopic niche modelling in Paper 1 relies upon Bayesian inference to provide robust accounting of uncertainty in model estimates. This is not the first time Bayesian mixing models have been applied to dietary studies in archaeology^{93,94}, but it is the first to apply them to understand seasonal patterns in dietary intake and the first to apply them on livestock.

Finally, the genetics of ancient livestock remain poorly described across Eurasia. The situation is better for sheep^{95,96}, cattle^{97–99}, and horses^{14,15}, but goats appear to have been

overlooked. Goats are critical animals for nomadic pastoralists, which are often used as fallback animals during times of hardship. Goats have higher environmental toughness compared to sheep and cattle, and they reproduce at higher rates, thus allowing herders to amplify herd sizes rapidly¹⁰⁰. While I applied a PCR-based approach in the mitochondrial genome, interesting results were obtained that will serve as a means to expand the study with more samples and taxa, and also to target nuclear loci, likely moving to a more sophisticated method using next-generation sequencing technology.

Taken together, the four papers of this dissertation reflect a number of methodological advances in Central Asian archaeology, ranging from providing greater clarity on social interaction along the Silk Roads to the earliest evidence for farming by pastoralists during the early third millennium BC. Each study emphasizes the distinctiveness of pastoralists in adapting to the environments of Central Asia and driving important cultural phenomena that greatly impacted human society in far-flung places. The following research adds valuable knowledge to our understanding of how this flexible way of life made it all possible.

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Paper 1



Received: 9 January 2018 Accepted: 5 March 2018 Published online: 26 March 2018

OPEN Urban and nomadic isotopic niches reveal dietary connectivities along **Central Asia's Silk Roads**

Taylor R. Hermes 1, Michael D. Frachetti³, Elissa A. Bullion³, Farhod Maksudov⁴, Samariddin Mustafokulov⁵ & Cheryl A. Makarewicz^{1,2}

The ancient 'Silk Roads' formed a vast network of trade and exchange that facilitated the movement of commodities and agricultural products across medieval Central Asia via settled urban communities and mobile pastoralists. Considering food consumption patterns as an expression of socio-economic interaction, we analyse human remains for carbon and nitrogen isotopes in order to establish dietary intake, then model isotopic niches to characterize dietary diversity and infer connectivity among communities of urbanites and nomadic pastoralists. The combination of low isotopic variation visible within urban groups with isotopic distinction between urban communities irrespective of local environmental conditions strongly suggests localized food production systems provided primary subsistence rather than agricultural goods exchanged along trade routes. Nomadic communities, in contrast, experienced higher dietary diversity reflecting engagements with a wide assortment of foodstuffs typical for mobile communities. These data indicate tightly bound social connectivity in urban centres pointedly funnelled local food products and homogenized dietary intake within settled communities, whereas open and opportunistic systems of food production and circulation were possible through more mobile lifeways.

Medieval Central Asia (ca. AD 2nd–16th c.) was a locus of extensive cultural and economic interaction between East Asia, the Middle East, and Europe through a vast network of overland trade routes, commonly called the 'Silk Roads'1-4. Urban centers, located in fertile oases and often described by archaeologists and historians alike as cosmopolitan cities^{5,6}, helped anchor Silk Road exchange and foster early globalization across Asia^{7,8}. Although settled communities provided a substantial economic foundation through agricultural output and the manufacture of valuable craft commodities such as metals, ceramics, glass, and textiles 9-14, mobile pastoralists also had strong influence on the trade system as operators of highland pathways that were based on seasonal movements for herding livestock15.

While transfers of objects and materials have long represented the intensity and scope of Silk Road exchange 16, we still lack detailed data about the way food systems, which reflect sustained engagements with the environment and broader community dynamics, were influenced by these far-reaching economic networks. Medieval Central Asia was defined by unusually diverse multicultural intersections, sudden social upheavals, and frequent demographic movements (Supplementary Information 1), but fundamental and perhaps durable dealings with food remain unclear. Food is culturally expressive of ecological adaptation, social relations, ideology, and economy¹⁷⁻²¹. Resolving dietary diversity in ancient Central Asian foodways provides an opportunity to investigate subsistence models of 'nomadic' and 'urban' communities that, together, played key roles in transcontinental interaction

In Central Asia, which is characterized by strong seasonal climate and uneven distribution of resources on the landscape^{22,23}, there is high potential for dietary diversity among pastoralist communities. Mobile pastoralists

¹Institute for Prehistoric and Protohistoric Archaeology, Christian-Albrechts-Universität zu Kiel, Johanna-Mestorf-Straße 2-6, 24118, Kiel, Germany. ²Graduate School 'Human Development in Landscapes', Christian-Albrechts-Universität zu Kiel, Leibniz Straße 3, 24118, Kiel, Germany. ³SAIE Laboratory, Department of Anthropology, Washington University in St. Louis, CB 1114, One Brookings Drive, St. Louis, MO, 63130, USA. 4Institute for Archaeological Research, Academy of Sciences of Uzbekistan, Yahya Gulamov Street No. 70, Tashkent, 100000, Uzbekistan. ⁵Afrasiyab Museum, Islam Karimov Street No. 7, Samarkand, 114151, Uzbekistan. Correspondence and requests for materials should be addressed to T.R.H. (email: trhermes@gshdl.uni-kiel.de) or M.D.F. (email: frachetti@wustl.edu) or C.A.M. (email: c.makarewicz@ufq.uni-kiel.de)

heavily subsist on livestock herding but also draw from a variety of food resources beyond domesticated animal products, including cultivated cereals, wild plants, fishes, and hunted game, which are exploited and consumed at varying intensities depending on environment, seasonal availability, mobility, and social networks^{24–28}. On the other hand, medieval urban food systems were strongly invested in cereal agriculture, food storage, and sedentism^{29,30}, and were subject to powerful political and religious institutions⁷, which may have generated less diverse dietary repertoires. However, dynamic commercial, political, and social activities between population centers and peripheral settlements, in addition to transactions with pastoralists, could have greatly expanded food availability and choice, as people and provisions, such as grains and live animals, regularly moved between urban and nomadic domains^{31–35}.

We consider community-level dietary breadth over long periods of human life history to be a marker of dietary connectivity, which represents the cultural integration of food production, distribution, and consumption among individuals. Through globalization processes, which involve growing economic networks between increasingly distant communities, cultural differences diminish as groups cooperate and synchronize their consumption patterns, whether of foods, styles, or ideas³⁶. In contemporary societies, globalized food economies expand with production standardization and increased dietary uniformity^{37,38}. Along these lines, high intra-community dietary variability indicates that community members maintained divergent connections to food resources that express individual dietary preferences and group partitioning. Conversely, low dietary variability within communities signals converged trajectories of foods that reflect shared dietary practices and socio-economic coordination.

In order to establish diversity in human dietary intake in Central Asian urban and nomadic communities, we analysed the carbon and nitrogen stable isotopic composition of bone collagen from human remains of 74 individuals (Table 1). Carbon and nitrogen stable isotope ratios (δ^{13} C and δ^{15} N) provide an integrative measure of dietary intake^{39,40}, and human bone collagen reflects a 10–15 year rolling average of protein consumption^{41–43}. We model isotopic niches in bi-variate isotopic space (δ -space) to estimate the breadth and structure of community-level diets based on intra-group variation across both dimensions of isotopic ratios simultaneously^{44,45}. Food resources with distinct isotopic content, which are incorporated into individual diets in various proportions, drive community dietary breadth⁴⁶. The isotopic niche modelling uses Bayesian inference to fit standard ellipses to data points that are then expressed as probability distributions of area (∞) and position in δ -space⁴⁷. Crucially, we performed redundancy analysis to unravel isotopic diversity driven by culturally defined food choices from environmental variables that influence the isotopic composition of food resources.

Isotopic variation in Central Asia. We sampled 14 cemeteries associated with medieval Silk Road communities that span a long transect of Central Asian geography to include present-day Kazakhstan, Uzbekistan, and Turkmenistan (Fig. 1). The human individuals analysed in this study represent urban and non-urban consumers, who potentially had access to substantial food options that were available through prolific agricultural systems and marketplaces that drew in people and foodstuffs from oasis, desert, steppe, and highland environments (Supplementary Information 2). Diverse food remains were recovered from the sites represented in this study, which included cereals, legumes, fruits, fish, and livestock (Supplementary Information 3).

Pronounced variation in the regional environments and topographies, combined with strong seasonality, in which these sites are situated, confers high isotopic variation in Central Asian foodwebs accessed by people. Vegetation communities range from cool montane meadows and forests consisting of largely C_3 taxa to hot low-land deserts that support both C_3 and C_4 plants^{48–51}, which exhibit (pre-modern^{52,53}) $\delta^{13}C$ values of $-25\pm2-5\%$ 0 and $-11\pm1\%$ 0, respectively^{54–57}. Food crops exploited in medieval Central Asia included the full spectrum of Eurasian domesticates including C_3 taxa, such as wheat, barley, rice, nuts, and fruits, and C_4 taxa, such as millets⁵⁸. Although nitrogen isotopic variation in vegetation communities in Central Asia is under-characterized, research in ecosystems comparable to those of Central Asia, such as the Gobi steppe-desert⁵⁹, the steppe deserts of the Caspian Depression⁶⁰, and semi-arid western Loess Plateau⁶¹, demonstrate wide variation in plant $\delta^{15}N$ values, ranging from -5 to 14‰, due to differences in local soil nitrogen pools and animal stocking rates^{62–65}. In general, fish exhibit high $\delta^{15}N$ values relative to terrestrial fauna^{66,67}, and in Central Asia, fish exhibit an apparent continuum of $\delta^{13}C$ values from ca. -11.5% to -27%68.

Results

Human remains in this study represent two chronological intervals of the medieval period. The bulk of the data-set (n = 63) dates to a 'mid-late' period of 6^{th} – 13^{th} c., which were recovered from sites in southern Kazakhstan, Uzbekistan, and western Turkmenistan. A small sample (n = 11) dates to an 'early' period of nomadic occupation at sites in southern Kazakhstan, which allows for a diachronic comparison of nomadic dietary intake within this region. Overall, human isotopic values range from ca. -20% to -10.5% for δ^{13} C and 9% to 15% for δ^{15} N (Fig. 2a). Isotope values cluster in both δ^{13} C and δ^{15} N for urban communities on a regional basis, while pastoralist communities from later periods exhibit wide distributions of δ^{13} C values and relatively narrow ranges of δ^{15} N values. Subsequent analyses using Bayesian inference clarified isotopic differences among communities while factoring in uncertainty due to small sample sizes. Summary statistics of isotopic data are provided in Supplementary Figure S1 and Table S1; raw isotopic data are provided in Supplementary Tables S2–S4.

Human isotopic variation across medieval Central Asia. Significant distinctions in the dietary intake of medieval urban and nomadic communities across Central Asia are revealed by Bayesian means (mean_b) of δ^{13} C and δ^{15} N values. Sharp dissimilarities are observed between urban communities located south of the Syr-Darya river, which provides a rough environmental boundary between the semi-arid/mountain steppe land-scapes in southern Kazakhstan and sandy desert landscapes interspersed with oases and foothill zones to the east. Significant differences in the 95% CIs of isotopic values from each southerly community, with the exception of West Pamir-Alay and Tashkent, are present with mean_b δ^{13} C values of -19.9% for Dehistan, -18.1% for West

Country	Region	Site	Elevation (m.a.s.l.)	Chronology	n	Archaeological context	References
Uzbekistan	West Pamir-Alay	Tashbulak	2100	9th–11th c.	4	Highland urban complex of the Qarakhanid Empire; citadel, metal workshops, necropolis; 7 ha	86,120
		Alyntepe	475	10th-13th c.	1	Provincial city with fortified walls and surrounding settlements; industrial scale brick and ceramic production; 40 ha	121
		Frinkent	530	10th-13th c.	4	Fortress complex with cemetery of unique Zoroastrian burials in large ceramic vessels; 14 ha	122,123
	Ferghana Valley	Chor Dona	580	11th-13th c.	4	Fortress mound with associated grain processing facility and ancillary ancient settlement of Andijan; estimated 10–15 ha	124,125
		Chartok	545	12th c.	11	Context information is not available	126
	Tashkent Oasis	Uturlik	270	12th c.	9	Large city with diverse economic production of crafts; along trade routes with Otrar; 60 ha	34,127
	Khoresm	Tok-kala	60	9th-12th c.	9	Urban fortress and surrounding settlements that functioned as a regional centre of political and economic influence; estimated 10–15 ha	128
Kazakhstan	Otrar Oasis	Konyr-tobe I	180	5th-7th c.	9	Cemetery platform raised 2.5 m above ground level on the outskirts of a fortress; burials suggest nomadic traditions	81,129
		Temirlanovka	320	2nd-4th c.	4	Cemetery unassociated with a settlement containing burials of nomadic individuals	SI 3
	Zhetysu (Semirech'ye)	Turgen II	1040	2nd-6th c.	7	Settlement and burial complex with nomadic occupations from the late Bronze Age to medieval period; estimated < 5 ha	79
		Butakty II	1150	10th-12th c.	6	Settlement and burial complex with nomadic occupations from the late Bronze Age to medieval period; estimated < 5 ha	80,130,131
		Karatal	620	8th-11th c.	3	Cemetery complex in use from the late Bronze Age to historical period; numerous nomadic encampment structures	84; SI 3
Turkmenistan	Dehistan Plain	Geotchik Depe	130	Iron Age*	2	Urban complex with occupation from the early Iron Age to late Islamic period; 5.5 ha	102,132,133
		Misrijan	170	11th-12th c.	1	One of numerous large villages in the Misrijan Oasis; precise site is not reported in the literature	102,132,133

Table 1. Geographic and archaeological information about analysed sites, including number of human samples. Detailed archaeological information for each site is provided in Supplementary Information 3. *See methods.

Pamir-Alay, -17.5% for Tashkent, -16.3% for Ferghana, and -13.3% for Khoresm (Fig. 2b; Information 4). Regional communities in Uzbekistan and Turkmenistan fall into in three trophic groups, each separated by ca. 2% in mean_b δ^{15} N (Fig. 2c).

A diachronic shift in the dietary intake of nomadic communities located in southern Kazakhstan is indicated by a significant 3‰ decrease in mean_b δ^{13} C values between early and late Otrar (Fig. 2d; Supplementary Information 4) and an increase of ca. 2‰ in mean_b δ^{13} C between early and late Zhetysu. However, mean_b δ^{13} C for late Zhetysu has a wide 95% CI between -15.9 and -12.3‰, which precludes a reliable estimate of the change. Overall, mean_b δ^{15} N for communities in southern Kazakhstan are more mutually similar to each other than that in southerly regions (Fig. 2c,e). Early Otrar displays mean_b δ^{15} N that is spaced apart by slightly less than ca. 1.7‰ from that of early Zhetysu, while in the later period the regions have identical mean_b δ^{15} N of ca 12‰.

Environment and isotopic variation. Isotopic patterns observed at individual archaeological sites are not driven by environmental inputs. Redundancy analysis between mean δ^{13} C and δ^{15} N values per cemetery site and 25 environmental parameters of ecologically relevant rainfall and temperature variations, in addition to elevation and soil properties, did not result in statistically significant relationships. Multiple linear regressions were also performed, which further failed to generate statistically significant relationships. (See Supplementary Information 5 for methods and results.)

Isotopic niche modelling. Central Asian medieval communities display isotopic niches that cluster in two distinct size ranges (Fig. 3; Supplementary Information 6). Group 1 exhibits small areas between 0.1 and 3.7‰² for urban communities in Uzbekistan and Turkmenistan, as do nomadic communities in southern Kazakhstan from the early medieval period. Over the next several hundred years, dietary diversity among individuals in Zhetysu and the Otrar Oasis (Group 2) appears to have radically increased, with isotopic niches estimated between 2.7 and 15.7‰². Notably, the greatest intra-community dietary diversity is visible in late Zhetysu, indicated by a 95% CI exceeding that from Group 1 communities, except early Otrar, which slightly overlaps by 0.7‰².

While all narrow, modelled isotopic niches for medieval urbanites in Uzbekistan are highly unique in orientation and position in δ -space (Fig. 4a). For late Zhetysu and Otrar, the diffuse spacing of isotopic values indicates exceedingly varied dietary intake. Individuals in late Zhetysu, which represent two archaeological sites, fall within the isotopic niches for Khoresm, Ferghana and Tashkent. Likewise, individuals in late Otrar, which represent one site, span all four urban isotopic niches from Uzbekistan. In contrast, there is substantial proportional overlap between the small isotopic niches from early Zhetysu and Ferghana and also early Otrar and Khoresm, respectively (95% CI: 0.13–0.64 and 0.17–0.69; Supplementary Fig. S6), which indicates a high likelihood of dietary parity.

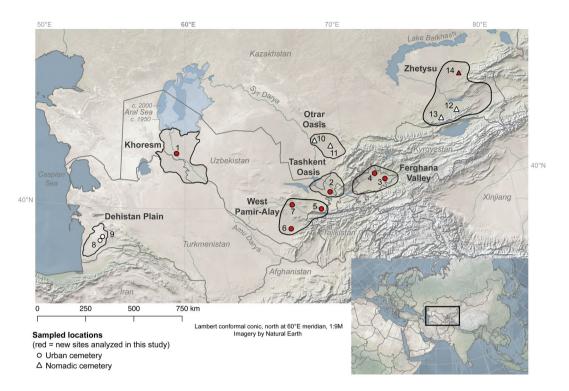


Figure 1. Map of Central Asia showing sites and regions with human stable isotopic data (δ^{13} C and δ^{15} N) analysed in this paper. Uzbekistan: 1) Tok-kala, 2) Uturlik, 3) Chor Dona, 4) Chartok, 5) Tashbulak, 6) Altyntepe, 7) Frinkent; Turkmenistan: 8) Geoktchik Depe, 9) Misrijan; Kazakhstan: 10) Konyr-Tobe, 11) Temirlanovka, 12) Turgen, 13) Butakty, 14) Karatal. Map generated with Quantum GIS, version 2.18.2 (https://www.qgis.org), using public domain data from Natural Earth (http://www.naturalearthdata.com).

Isotopic niches from urban communities in Uzbekistan illustrate strong dissimilarity from each other (Fig. 4b). The highest proportion of niche overlap occurs between West Pamir-Alay and Ferghana (95% CI: 0.05–0.36) and between West Pamir-Alay and Tashkent (95% CI: 0.01–0.32), suggesting that a maximum of one-third of individuals in these communities had similar dietary intake. However, this niche overlap could be as low as 1–5%. The remaining pairwise comparisons of urban communities show negligible occurrence of overlap (Supplementary Information 7).

Discussion

Taken together, urban and nomadic communities display distinctive but wide-ranging isotopic values that are strongly suggestive of diverse dietary intake across medieval Central Asia. A large overall range of human $\delta^{13}C$ values from ca. -20 to -11% is likely due to individuals consuming mostly C_3 crops (wheat, barley, and rice) or C_4 millets at sustained intensities. Among Eurasian cultigens, millets are isotopically distinct with high ^{13}C concentration. Millets thrive in hot and arid climate and exhibit fast-growing and drought-tolerant adaptations 69 , traits which would have provided Central Asian farmers and mobile pastoralists opportunities for low risk, low-investment cultivation in marginal agricultural areas 70,71 . The natural abundance of C_4 vegetation is substantially higher in the desert zones of Central Asia 50 , where livestock, as part of urban or nomadic subsistence, could have accessed enriched $\delta^{13}C$ biomass and provided human consumers with protein-dense foods (meat and milk) with high $\delta^{13}C$ values. A lack of correlations between human isotopic values and site environmental parameters suggests that dietary intake across the region was shaped primarily by food choice. Medieval agriculture in Central Asia, which used complex crop schedules and large irrigation works $^{71-76}$, likely enabled productivity to overcome environmental constraints on crop variety in order to meet the inter-connected dietary demands of consumers.

Modelled isotopic niches indicate that nomadic communities exploited a wide variety of dietary resources, while urban communities engaged in more limited dietary repertoires. The small isotopic niche sizes documented among urban communities in Uzbekistan and Turkmenistan suggest food channels that were shaped via consistent and insular dietary connectivity. On the other hand, large isotopic niches in southern Kazakhstan from a relatively contemporaneous period indicate that a multitude of food acquisition strategies were in use, by which communities tied more closely with pastoral nomadic lifeways comprised individuals with assorted dietary relationships that led to sustained differences in isotopic variability. The dietary connectivity for these nomadic groups may have fostered group partitioning through unsynchronized food interactions among different community members. The small isotopic niches for nomadic communities in early Otrar and Zhetysu, which in this case substantially overlap with that for Khoresm and Ferghana, suggesting more restricted dietary intake by pastoralists, emphasize the subsistence plasticity of pastoral nomads who readily contour their own food production and interaction networks in response to dynamic social and natural landscapes^{24,26,77}.

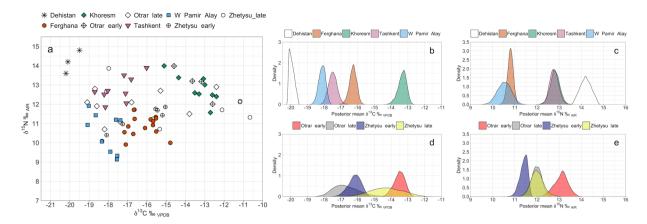


Figure 2. (a) Human carbon and nitrogen isotopic ratios from medieval Central Asia; (**b-c**) Posterior probability distributions of isotopic means obtained by Bayesian bootstrapping (mean_b) from medieval urban communities in Uzbekistan and Turkmenistan and (**d-e**) from medieval nomadic communities in southern Kazakhstan.

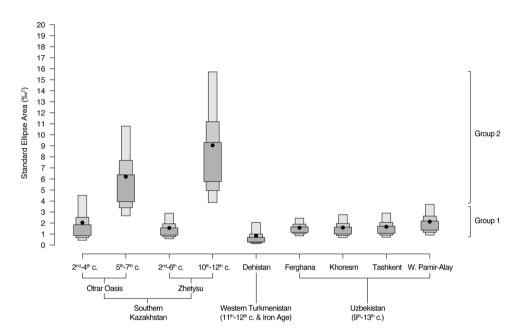


Figure 3. Community-level dietary diversity of medieval humans represented by posterior distributions of core isotopic niche area ($\%^2$) by sites and regions in Central Asia. Isotopic niches were calculated by fitting standard ellipses to cover ca. 39% of the δ^{13} C and δ^{15} N data points using Bayesian inference. Black dots indicate area means, and the shaded boxes, from dark to light, represent the 50%, 75%, and 95% credible intervals.

The diachronic shift in isotopic niche size between early and late nomadic communities also highlights two distinct scales of dietary variability that illustrate the importance of multi-resource pastoralism to Silk Road interactions. In southern Kazakhstan, the early medieval period is marked by a growth of urban centres, villages, and agricultural economies^{78–81}, which is also historically associated with frequent conflict among nomadic confederacies that instigated socio-political turmoil^{1,82}. In order to mitigate risk and take advantage of economic opportunities presented by these newly founded centres, nomadic communities likely participated in coordinated subsistence interactions with settled populations over short distances, which would have effectively limited access to diverse food resources and thus narrowed their dietary breadth. During the strengthening of Turkic empires several centuries later^{1,3,31,83}, Silk Road trans-regional trading expanded to include bulk commodities and raw materials³², and nomadic communities across southern Kazakhstan expressed wide dietary breadth, as indicated by large isotopic niche sizes.

One explanation for greater inter-individual dietary diversity during this later medieval period is that nomadic communities tapped into growing trade economies as agents of food exchange and broke out of insular urban subsistence channels. Recent excavations of nomadic encampments in the foothill zones of West Pamir-Alay and Zhetysu illustrate highly variable levels of economic interaction between pastoralists and urban centres. At these

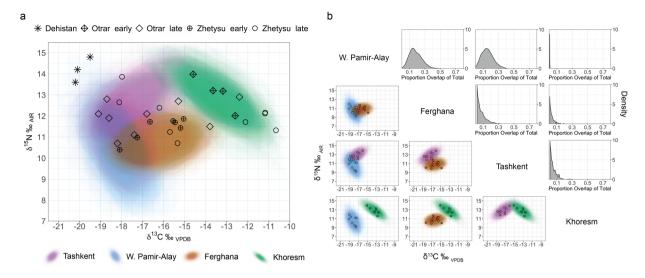


Figure 4. (a) Medieval urban isotopic niches from Uzbekistan are displayed as probability clouds, and individual isotopic values from southern Kazakhstan (nomadic communities) and western Turkmenistan (urban community) are represented as points. (b) Isotopic niche overlap analysis for urban communities in Uzbekistan. Standard ellipses covering 95% of δ^{13} C and δ^{15} N values were modelled using Bayesian inference. Overlapping areas for each pairwise comparisons in δ -space were visualized as probability clouds with underlying isotopic data points superimposed (lower left). Area overlap of total isotopic niche area for each pair was plotted as probability distributions (upper right).

sites, cultural materials associated with 8th–13th c. radiocarbon chronologies include cotton fabrics⁸⁴ and variable mixtures of ceramics ranging between standardized wheel-spun food storage vessels from distant oases communities and locally produced 'handmade' coarsewares, which are rare in urban contexts^{85,86}. The presence of hybrid ceramic assemblages and cotton, a woven trade good associated with oasis production centers^{87,88}, suggests that complex and non-uniform relationships with urban economies coincided with intra-group dietary diversity in mobile pastoralist communities²⁵.

Accordingly, at the community level, a second scale of dietary variability that is representative of multi-resource pastoralism is observed at late Otrar and Zhetysu, which display wide ranges of δ^{13} C values (Fig. 4a). Some individuals in late Zhetysu have δ^{13} C values similar to those commonly observed in humans from prehistoric millet-based farming societies in China, where millets were domesticated⁸⁹⁻⁹¹, while individuals in late Zhetysu and Otrar had low δ^{13} C values, typical of Neolithic and early Bronze Age humans before millet spread to the C_3 -dominant Central Asian steppe⁹². Both communities in late Otrar and Zhetysu display similar δ^{15} N distributions, though individuals exhibit differences in dietary intake of relative proportions of meat and dairy products (Fig. 2e). Together, these findings suggest that dietary connectivity at the steppe margins was associated with an ecumene of diverse food consumption, in which individuals maintained separate subsistence strategies as they simultaneously participated in a common nomadic ethos. Compared to urbanites, mobile pastoralists likely maintained closer control of food production and distribution, allowing them to eat according to food preferences, which may have been less important for maintaining social ties than in urban contexts.

The combination of narrow dietary niches with isotopic distinction in human remains from medieval urban communities south of the Syr-Darya river is due to trophic-level variation in the intensity of meat and cereal consumption between communities as well as differences in the contribution of millet to urban diets, either eaten directly or indirectly obtained from meat and dairy of animals foddered with millet. Isotopic niche overlap was highest for urban communities in close geographic proximity to one another, a pattern that suggests neighbouring communities either participated in similar food traditions or agricultural practices that were confined to small catchments. These communities may have participated in limited inter-regional trading of staple foods, which likely would have moved through established subsistence channels as if locally produced. There is also the possibility that dietary connectivity in urban contexts was subject to bureaucratic intermediaries, which exerted influence through land tenure and taxation^{1,32,93}. Alternatively, in the absence of top-down control, food exchange networks may have steadily channelled provisions to urbanites as a reflection of other economic networks that inevitably developed to be streamlined towards cultural insiders in cosmopolitan contexts.

While the consensus among historians and archaeologists is that urbanites in medieval Central Asia dwelled in rich multicultural settings 5,7,16 , there appears to be a limit to this diversity in dietary intake as revealed through isotopic niche modelling. Distinctions in food choice and diet between urban communities suggest regional food repertoires were narrowly circumscribed, at least between C_3 and C_4 crops and also between animal and plant protein. Regional patterns in diet imply that cultural differences surrounding foods may have been surprisingly diminished within urban communities, which runs counter to the notion of collective cosmopolitanism in medieval Central Asia. Medieval urbanites in Central Asia maintained inward-focused dietary connectivity that likely generated a localized social cohesion through culturally integrated supply chains for consumers.

Scholars also associate Silk Road activity with early globalization processes^{7,8}, in which urban centres are viewed as the main drivers of cultural influence and outward economic connectivity, while 'nomads' are interpreted as antagonists to ancient civilization^{94–96}. Yet, through multi-resource subsistence strategies, nomadic communities likely wielded flexible economic engagements that traversed open landscapes of contact with people who facilitated far-reaching connectivity. In this sense, nomadic individuals may have been more culturally interoperable and able to participate in, disengage from, and influence cultural spheres more easily than urban populations. Indeed, many of the pan-regional turnovers in religion, language, and political authority that resulted in changes in architecture, technologies, and other commodity classes in the medieval period are historically described as nomadic innovations^{1,2,31}, and essential routes that connected Silk Road sites in the highland regions of Central Asia were likely shaped by nomadic mobility¹⁵. This study takes a new step toward resolving the complex interplay between urban and nomadic societies that are rarely available through archaeological datasets. Establishing dietary diversity provides an emerging understanding of food and connectivity along Central Asia's Silk Roads that highlights the significance of ancient nomadic pastoralists in bridging seemingly insulated urban centres.

Materials and Methods

Human remains. We performed new analyses on human remains from Uzbekistan and Kazakhstan, which were selected based on 1) medieval chronology from ca. 8^{th} – 13^{th} c., 2) information on archaeological context, and 3) minimum age estimation of young adult. The majority of human remains analysed from Uzbekistan (n = 38) were excavated at various times over the past 80 years and do not include associated post-cranial elements. Human remains from Tashbulak (n = 4) were excavated in 2015 and are represented by complete inventories of skeletal elements. Human remains from Uzbekistan are stored in the Institute of Archaeology of the Uzbek Academy of Sciences in Samarkand, under the auspices of the Archaeology of the Qarakhanids Project (Co-PIs: Farhod Maksudov and Michael Frachetti). Human remains from Karatal (n = 3) were excavated in 2006 and 2008 and include incomplete skeletal elements due to ancient burial looting and modern erosion (Supplementary Information 3). Human remains from Karatal are stored at the Central State Museum of Kazakhstan in Almaty, under the auspices of the Dzhungar Mountain Archaeology Project (Co-PIs: Alexei Mar'yahshev and Michael Frachetti). A list of human samples is provided in Supplementary Tables S2–S4.

Isotopic analysis. Approximately $1-2\,\mathrm{cm}^3$ of sample were cut from dense cortical bone. Collagen extraction was performed in the Archaeological Stable Isotope Laboratory of Kiel University following Tuross *et al.*⁹⁷. Mass spectrometry for δ^{13} C and δ^{15} N was performed at the Boston University Stable Isotope Laboratory using a EuroVector Euro EA elemental analyser coupled with a GVI IsoPrime in continuous flow mode with an analytical error of 0.1% and 0.2% for δ^{13} C and δ^{15} N, respectively. Isotopic values are reported in permil (%) relative to the Vienna Pee Dee Belemnite (VPDB) standard for δ^{13} C and atmospheric nitrogen (AIR) for δ^{15} N. Collagen samples with an elemental C:N ratio less than 2.9 or greater than 3.6 were considered diagenically altered and unsuitable for inclusion $^{98-100}$. Failed samples (n = 3) are reported in Supplementary Table S5.

Previously published δ^{13} C and δ^{15} N values of human bone collagen from southern Central Asia were analysed (Supplementary Tables S3-S4). Isotopic data from medieval southern Kazakhstan included 13 samples from the Otrar Oasis (3rd-7th c.) and 13 samples from southern Zhetysu (2nd-12th c.)¹⁰¹. Data from the Dehistan Plain in western Turkmenistan included two samples from the Iron Age (ca. 1300 BC) and one sample from the medieval period (ca. 11th-12th c.)¹⁰². These data were lumped together irrespective of chronology due to low sample size for the region and similar isotopic values, which were unique in our dataset.

Human collagen is δ^{13} C enriched by ca. 1–3% relative to the carbon isotope composition of consumed foods¹⁰³, whereas herbivores are enriched in δ^{13} C by ca. 5% relative to consumed vegetation^{104,105}. Human nitrogen isotope values reflect the intensity of cereal versus meat consumption, as there is a 2–5% trophic enrichment in δ^{15} N with each step up in the food web^{40,106,107}, but also reflect variation in food production systems that introduce exogenous nitrogen, usually in the form of manure, to the floral base of the food web, potentially imparting considerable nitrogen isotopic variation in agricultural and livestock food^{62,63,65,108,109}. In attempts to estimate the relative contribution of specific foods in diets, a common approach in archaeological dietary studies is to sample ancient and modern plants and animals to assess possible isotopic variability in food sources that result from various environmental and anthropogenic factors¹¹⁰. For the purposes of establishing human dietary diversity at the community level, however, knowledge of the isotopic content of ancient food remains is unnecessary.

Statistical analysis. All statistical analyses were performed using R, version $3.4.0^{111}$. Due to low sample sizes per site $(1 \le n \le 11)$, $\delta^{13}C$ and $\delta^{15}N$ values were analysed by geographic region $(3 \le n \le 15)$ using Bayesian techniques to quantify uncertainty and overcome issues with non-parametric data distributions, which cannot be reliably analysed with frequentist methods. The means of isotopic values for each region were calculated with a Bayesian bootstrapping method at 5000 iterations using the package bayesboot¹¹². Posterior distributions of means for each group were considered statistically different from one another if the 95% credible intervals (CI) did not overlap.

Isotopic niche modelling. Isotopic niches were analysed using SIBER (Stable Isotope Bayesian Ellipses in R), version $2.1.3^{47}$. The Markov chain Monte Carlo simulation was run with uniform priors 2,000,000 times, with the first 10,000 results discarded (burn-in), followed by a 1:100 thinning. The fitted ellipses express a posterior probability distribution of area (‰²) and position in δ-space. This technique is statistically advantageous for analysing communities of consumers, as fitted ellipses are less sensitive to sample size than other spatial metrics, such as convex hulls⁴⁷, and uncertainty is factored into estimates, such as sample size, which has previously challenged studies using a finite number of specimens from the archaeological record. Isotopic niches were compared among

regional groups by using the Bayesian standard ellipse areas (SEA_b) and the proportion of SEA_b overlap as total SEA_b pairwise for each region. Overlapping areas of isotopic niches indicate similarity in isotopic inputs and thus comparable resource exploitation $^{113-115}$.

Environmental modelling and GIS. Interactive effects between human stable isotope values and environmental parameters at each site in 10 km and 50 km spatial buffers were explored using redundancy analysis (RDA) with the R package vegan, version 2.4–5¹¹⁶. Environmental parameters included elevation, bioclim data¹¹⁷, which are derived from monthly temperature and rainfall values from 1970–2000, and soil parameters obtained from the Soil Grid Project¹¹⁸. (See Supplementary Information 5 for RDA methods and results.) Data were mapped using Quantum GIS, version 2.18.2¹¹⁹. Base imagery in Fig. 1 was obtained from Natural Earth (http://www.naturalearthdata.com).

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Acknowledgements

We especially thank Amridin Berdimuradov, the director of the Institute of Archaeology in Samarkand (National Academy of Sciences of Uzbekistan) for his continued support and enthusiasm for this project and international collaborations in general. We also thank Dima Voyakin for providing access to archaeological reports on Temirlanovka and for his help facilitating research in Kazakhstan. Recognition is also due to Marc Meyer and Mellissa Murphy for providing osteological data for the human individuals excavated from the Karatal cemetery complex. A special thank you goes to Malte Rühlemann for assisting with the redundancy analysis. Funding for this research was provided by the Graduate School 'Human Development in Landscapes' at Kiel University for the doctoral research of Taylor Hermes. Research at Tashbulak was funded by the National Geographic Society, the Max van Berchem Foundation, and Washington University in St. Louis. We are grateful for support from the Open Access Publikationsfonds of Land Schleswig-Holstein. Finally, we thank two anonymous reviewers for their suggestions on improving this paper.

Author Contributions

T.R.H. designed and initiated the research. T.R.H., E.A.B., F.M., and S.M. conducted sample collection. E.A.B. performed the osteological analysis of human remains and, with T.R.H., described sites in Uzbekistan for the supplementary information. T.R.H. wrote the remaining supplementary information. T.R.H. prepared specimens for stable isotope analysis and conducted the data analysis. T.R.H. and C.A.M., and M.D.F. interpreted the results. T.R.H., M.D.F., and C.A.M. wrote the manuscript.

Additional Information

Supplementary information accompanies this paper at https://doi.org/10.1038/s41598-018-22995-2.

Competing Interests: The authors declare no competing interests.

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Supplementary Information

Urban and nomadic isotopic niches reveal dietary connectivities along Central Asia's Silk Roads

Taylor R. Hermes^{1,2}*
Michael D. Frachetti³*
Elissa A. Bullion³
Farhod Maksudov⁴
Samiriddin Mustafakulov⁵
Cheryl A. Makarewicz^{1,2}*

* Corresponding authors

Affiliations

1 Graduate School 'Human Development in Landscapes' Christian-Albrechts-Universität zu Kiel Leibniz Straße 3 24118 Kiel, Germany trhermes@gshdl.uni-kiel.de c.makarewicz@ufg.uni-kiel.de

2 Archaeological Stable Isotope Laboratory Institute for Prehistoric and Protohistoric Archaeology Christian-Albrechts-Universität zu Kiel Johanna-Mestorf-Straße 2-6 24118 Kiel, Germany

3 SAIE Laboratory Department of Anthropology Washington University in St. Louis One Brookings Drive, CB 1114 St. Louis, MO 63130, USA elissa.bullion@wustl.edu frachetti@wustl.edu

4 Institute for Archaeological Research, Academy of Sciences of Uzbekistan Yahya Gulamov Street No. 70 Tashkent, 100000, Uzbekistan fmaksudov@yahoo.com

5 Afrasiyab Museum Islam Karimov Street No. 7 Samarkand, 114151, Uzbekistan m samar@rambler.ru

Supplementary Information 1: Culture history of increased interaction in medieval Central Asia

From the 2rd to 6th c., the earliest dates of our human samples, Central Asia was characterized by ethnically diverse and politically independent city-states, occasionally subjugated by distant powers, that maintained sustained interactions with Turkic nomadic groups located in the steppes of present-day Kazakhstan, Uzbekistan, and Xinjiang¹. During the 7th-8th c., the Islamic political authority spread into the settled oases of the Silk Road system^{1,2}, which is associated with a strengthening of the social integration between institutions in urban economies³, expansion of long-distance trade⁴, and mutual commercial prospects for nomads and urbanites^{2,5}.

By the 9th-10th c., Central Asia was generally divided between the Samanids, an Islamic dynasty of Persian origin that controlled lowland oases, and Turkish-speaking nomadic hegemonies native to the steppe and highland zones^{6,7}. In the 10th-11th c., the Qarakhanids, an imperial confederacy of nomadic lineages, conquered Central Asia and populated urban institutions with its nobility, which expanded urban projects and, supposedly, was followed by an influx of peasant nomads into cities and villages but a concurrent political expansion into highland zones^{1,2,8,9}. The Qarakhanids continued to rule Central Asia until about the mid-12th c. when the empire fragmented^{1,7}, and the Mongols swept over the region in the early 13th c.^{1,10}, which marks the nearest historical boundary of our study.

Supplementary Information 2: Subsistence review for medieval Central Asia

The food production systems of medieval Central Asia were supported by sophisticated irrigation technology as well as extensive rainfed farming and livestock management that, together, generated a diverse and plentiful supply of crops and animal products to both urban and nomadic realms^{11–15}. Ancient texts of Chinese and Arab geographers describe lush Central Asian oases where wheat, barley, millet, rice, peas, chickpeas, lentils, melons, and cotton were cultivated, in addition to gardens, vineyards, and orchards of fruit and nut trees^{1,16,17}. Incidental recovery of carbonized botanical remains from archaeological sites and ubiquity of agricultural artefacts confirm these cultigens were grown and processed throughout the region^{18–24}. More systematic recovery of botanical remains confirms a rich diversity of cultivated taxa with a strong emphasis on various grains as staple foods^{25–29}, alongside local pastoral production and, presumably, animal products acquired from local nomadic herders^{18,30,31}.

The historical record further documents bustling fairs and markets in which foods were traded in bulk and also exchanged in quantities for individual households or estates. The geographic extent of this commerce has been documented through ceramics artefacts, which derive from major urban production centers in Samarkand, Tashkent, Bukhara, Afghanistan, Iran, China and beyond 1,6,18,31. One of the most prominent markets took place in the Zaamin Mountains., in a city called Marsmand, which was supposedly located next to a major centre for mining ore and metal production named Mink 18,19. While existing textual accounts and subsistence datasets have provided insights into interactions with food in urban centers and fortified settlements, no published data exists to elaborate upon subsistence for nomadic pastoralists in later medieval times. Inconsistent chronologies, geographic coverage, and recording methods preclude using existing data to understand regional dietary diversity and food exchange tied to the historical record.

Supplementary Information 3: Sampled sites, archaeological context, and subsistence data

Uzbekistan

Khoresm

Tok-kala is located near the modern city Nukus in Khoresm. The fortress, settlement, and cemeteries that comprise the preserved site cover approximately eight hectares and are located on a raised hill above the floodplain of the Amu Darya. An ancient river channel runs along the base of the hill, and there is evidence of multiple flooding events throughout its history, which appear to have destroyed much of the settlement architecture. Flooding in Khoresm is periodic, which has catastrophic potential to alter the course of the Amu-Darya and affect the level of the Aral Sea, and the harnessing of these floodwaters is considered to be a critical component to the success of irrigation systems in Khoresm¹⁰. During periods of vast hydrological change, such as in the 4th c., settlement patterns were drastically altered and sites were abandoned³².

Archaeological materials recovered at Tok-kala seem to indicate significant interaction with nomadic groups in the region²¹. Besides a modern Muslim cemetery, there are three known cemeteries at Tok-kala²¹. The first is an early medieval (7th-8th c.) naos with ossuary burials, consistent with Zoroastrian practices. Notably, this phase contains well-preserved pieces of wall paintings and inscriptions on ossuaries that have led to speculation about their cultural origins, either directly from Sassanid roots or from older heritages pre-dating the Sassanid period³³. The other two burial grounds are middle medieval (9th-11th c.) Muslim cemeteries, identified from grave forms and body position of interred individuals. Samples in this study were recovered from individuals in Muslim burials. The first of these cemeteries is located on top of the earlier Zoroastrian burials. Despite its relatively small size, Tok-kala is sometimes known as a "besh-kala," or mother-city, of Khoresm, indicating past cultural significance. Tok-kala is considered to have been a regional centre of political and economic influence²¹.

The most comprehensive information about Tok-kala can be found in Gudovka's monograph²¹. She reports the recovery of wheat, barley, and millets from multiple cultural layers, but these macrobotanical remains were not quantified. Rich livestock and fish bones were also reported but were not quantified.

Tashkent Oasis

Uturlik sits on the left bank of the Syr Darya River in the Sirdarya Region of modern Uzbekistan, near Tashkent. In the historical and archaeological literature, the ancient city and local region are often referred to as Chach^{31,34}. The site area covers approximately 60 hectares, and was occupied from the 6th-12th c.³⁵, and our samples from the site date to the 10th-12th c. A large medieval Muslim cemetery of approximately 4,000 graves is located on the western side of the site. The large area of the settlement and cemetery at Uturlik have led researchers to estimate a total population of between 8 and 10 thousand people at its peak³⁵. The city is described as having a sprawling residential and artisan sections that provided a diverse and productive craft economy, in addition to vibrant markets³¹. Despite the apparent size of Uturlik, there is a paucity of detailed information in published sources about the ancient city. Scholars highlight the location of the city as being on an important trade route

between Samarkand, to the south, and the Otrar Oasis, located in Kazakhstan, which has led to speculation about interactions between settled and nomadic populations³¹. There does not appear to be any quantified subsistence information available for Uturlik, but scholars describe the ancient city as being supplied by irrigated and rainfed fields, in addition to livestock herding in the local hilly landscape³¹. There is the possibility that fishing occurred in the marshes, irrigation canals, and Syr-Darya river³¹, but there is no material evidence for fishing reported in the literature.

Ferghana Valley

Chor Dona is located in the southeastern region of the Ferghana Valley, on the northwestern outskirts of the city of Andijan. The site was occupied during two periods: 7^{th} - 8^{th} c. and 14^{th} - 16^{th} c. 36 . Between these two occupations, the site was used as a cemetery. The majority of burials at Chor Dona are typical of Muslim practice, but there are at least five individuals buried with objects and grave structures similar to pre-Islamic rituals common in medieval sites in Kazakhstan associated with nomadic groups 36 . Chor Dona's proximity to ancient Andijan would have likely put its residents within the economic and social sphere of this large urban centre.

Chor Dona appears to have served as a large-scale economic production centre for grains, as evidenced by flour milling facilities³⁶. Macrobotanical remains of foods recovered from the site include walnuts, millet, barley, and wheat, in addition to an assortment of agricultural tools associated with cultivation, harvesting, and processing³⁶. Furthermore, fruit seeds of grapes, cherry plums, peaches, and apricots were reported as ubiquitous in the site³⁶. Cotton seeds were also recovered³⁶.

Chartok is not well described in the archaeological literature. The site was published in a craniometric study on medieval populations in Uzbekistan that briefly describes Chartok as dating to the 12th c. and located in the Namangan region of northern Ferghana³⁴. Unfortunately, no cultural context is given about the site. Searches for additional information did not yield results.

West Pamir-Alay

Tashbulak is a recently discovered site located in the highlands of the Malguzar Mountains, close to the border with Tajikistan, at approximately 2100 meters above sea level³⁷. It is the only known highland centre that was constructed and occupied during the Qarakhanid Empire. This region has historically been occupied by nomadic groups, but during the 9th-13th c., a series of small cities and large villages were constructed in the mountain zone³⁸. Tashbulak consists of an elevated citadel above a lower town area with workshops and possible residencies⁹. The site also contains a large Muslim cemetery of approximately 400 burials⁹. The site spans from the 9th to early 12th c., which is currently dated according to coins and Qarakhanid ceramics⁹. Research at the site is ongoing, but the presence of iron objects, glazed and wheel made ceramics, and non-local fruits indicate the likelihood that Tashbulak served as an important market, trading post, and/or production centre between highland and lowland regions. Macrobotanical remains of grains recovered from the site include barley and wheat, and millets were not found⁹; detailed paleobotanical work is forthcoming by Robert Spengler.

Altyntepe is in the western part of the Kashgardarya Oasis, near the modern-day town of Karabag. Although it was founded in the 7th-8th c., the site reached its peak in the 10th-13th c. and covered about 40 hectares³⁹. The city consisted of a fortified inner city with surrounding sprawling settlements, and a cemetery is located on the southwest border of the site³⁹. The remains of several different craft workshops have been recovered, including industrial-scale brick and pottery production complexes³⁹. Despite evidence of economic fluorescence, some researchers point to the relatively small defensive walls as an indication that Altyntepe was not as important or wealthy as other medieval cities, such as Penjikent³⁹.

Macrobotanical remains at Alyntepe include watermelon, muskmelon, and grape seeds³⁹. Excavations recovered bulk remains of wheat, which were reported as club wheat (*Triticum compactum*)³⁹. Barley was not reported from Altyntepe, but small quantities were found in nearby sites³⁹. Animal bones present in ash deposits were found throughout the site³⁹. While fish bones were not reported, numerous ceramic bowls and dishes were recovered that were decorated with stamp impressions depicting slender symbols of fish³⁹.

Frinkent, also known as Afarinkend, is located in the lowlands of the Zerafshan valley, in the interfluve between the Kara-Darya and Ak-Darya rivers. Frinkent is sixty kilometres northwest of the city of Samarkand. The site, delineated by a wall, includes a fortress complex, cemetery, and settlement area covering approximately 14 hectares⁴⁰. The site was founded in the 7th century by the brother of the ruler of Samarkand, making it a site of potential political importance⁴⁰. The site continued to be an important centre of the Zoroastrian faith in the Zerafshan region even through the 10th century, when Islam had replaced most other faiths⁴¹. The cemetery at Frinkent is a stark example of this role. Hundreds of individuals were cremated or interred in large ceramic jars, some of which were painted on the exterior and had soot deposits as would have been caused by burning⁴⁰. Many of the jars contained the skeletal remains of multiple individuals, and often the mandibles were missing, indicating skeletonization before primary or secondary deposition in the vessels⁴⁰. Subsistence data could not be located for Frinkent.

Kazakhstan

Otrar Oasis

Konyr-tobe, also known as Kuyuk-Mardan, is a medieval fortress located on the Arys River. Two necropolises remain the only components of the site that have been systematically researched and published⁴². Konyr-tobe I contains 120 burials that were placed on a unique platform mound constructed from local clay-rich soil and mudbricks, which stands about 2.5 m above the ground level⁴². The platforms is outside of the fortress, and its association to the fortress is unclear. The human remains with stable isotopic data included in our study are sourced from these burials⁴³. Located about 40 m from Konyr-tobe II is a similar but smaller platform mound with 8 burials⁴². Regional specialists consider these platform cemeteries, which are widely distributed in the Arys valley and Otrar Oasis, to have been built in order to stand seasonal floods in the area that heavily saturate the takyr surface⁴⁴. This style of cemetery construction is unique to this site and scholars have interpreted it to represent nomadic communities⁴².

Konyr-tobe I was in use from the 5th-7th c. based on iron weapons and implements, in addition to ceramic vessels, interred with the bodies^{42,44}. Burial practices show resemblance

to pre-Islamic and late medieval rituals, despite artefacts largely reflecting an early medieval chronology^{42,44}. This burial variability suggests high levels of interaction with outlying communities, which is further demonstrated by distinctive ceramic vessels with spouts common in the Konyr-tobe assemblage that were also found nearly 800 km away in contemporaneous layers of a nomadic encampment site in the desert-steppe margin of the Dzhungar Mountains, named Mukri⁴⁵. In rooms of a nearby city, Kok-mardan, ceramic storage vessels were found with millet, wheat, barley, rice, and peas⁴², but subsistence data for Konyr-tobe or its cemeteries were not reported.

Temirlanovka is an early medieval burial site located on the northern bank of Arys River. The site contains 49 burial mounds that date to the 2nd-4th c. based on material inventories of the graves⁴⁶ and one individual that was directly radiocarbon dated (cal AD 140-376)⁴³. Most of the site remains unpublished, but an iron dagger from burial #33 has raised speculation that the community using the Temirlanovka burial ground had contacts with nomadic groups as far away as the Black Sea region, which during the late Iron Age can be generally described as a territory of the Scythian-Sarmatian cultural groups⁴⁷. Pollen analysis from sediments recovered from ceramic vessels found in the burials revealed natural background vegetation of Ephedra and Artemisia, in addition to a small number of pollen grains from buckwheat and legumes⁴⁶.

Zhetysu (Semirech'ye)

Turgen is a multi-period settlement and burial complex in the modern city Turgen. The site contains mostly late Andronovo to Wusun cultural phases, but there is are also early medieval burials, which further extend across the entire floodplain the Ili Valley⁴⁸. The burial forms include low earthen mounds surrounded by stone fences, which are characteristic of the Turkic period⁴⁸. The subsistence economy of the early medieval period is believed to be similar to that of the late Iron Age, which included dense villages, irrigation agriculture, and management of livestock⁴⁹. However, detailed excavation data for the site is not well reported. The chronology of the medieval burials is estimated to span the 2nd-6th c., according to burial forms and material remains that indicate nomadic traditions.

Butakty is a multi-period settlement and burial complex in the modern city Almaty. The site includes occupations from the late Bronze Age Andronovo cultural horizon (ca. 1700-1200 BC) to the medieval period (ca. AD 12th c.)^{50,51}. The settlement areas contain rich artefact assemblages and architectural remains that indicate intensive, perhaps year-round occupation at the site^{50,51}. The medieval burials are reported to be low in number, but they contain evidence of ritual practices common in the Zhetysu region, which includes burying sheep/goat limbs with the human bodies⁵¹. One individual from Butakty was directly radiocarbon dated to cal AD 1022-1155⁴³. Iron fasteners and ring pendants share style with those characteristic in nomadic groups in central Kazakhstan and the Altai region^{50,51}. No subsistence data could be located for Butakty, except brief mentions of an agro-pastoral economy that persisted throughout the site's occupational sequence^{50,51}. (Butakty had been previously published with the incorrect geographical coordinates that placed it 10 km east of Turgen⁴³, but its location has been corrected in our paper, as shown in main text Fig. 1 and Table 1.)

Karatal is a multi-period, ancient cemetery complex located on the foothills of the Dzhungar Mountains and is about 1 km from the Karatal River. The site underwent partial excavation and survey in 2006 by Alexei Mar'yashev, Taylor Hermes, and Marc Meyer, and three

periods of use were identified (unpublished report). In 2008, another campaign continued work on medieval burials. The first occupation occurred during the late Bronze Age (ca. 1700-1200 BC), as indicated by distinctive stone burial cists that contained cremated human remains and 'Andronovo'-style ceramics. Some of the burial cists were arranged in pairs and enclosed within a low-profile stone fence. The next occupation occurred during the Iron Age (ca. 1000 BC – AD 300), as indicated by linear rows of earthen mounds (kurgans) placed on the flat areas of rolling hills. These kurgans were not excavated. Within the site's environs, numerous rock outcrops were found to be decorated with panels of Bronze and Iron Age petroglyphs that depict animals and anthropomorphic figures, which are common in the Zhetysu region^{52,53}. Abandoned settlements, consisting of stone foundations for small structures (likely felt tents), were recorded on survey at low density, which suggests local residence by pastoralist groups.

The final phase of the Karatal cemetery complex occurred during the medieval period. The final phase of the Karatal cemetery complex occurred during the medieval period. Four adjacent burials containing the remains of children (0-3 years) radiocarbon dated to the 17^{th} - 19^{th} c. (unpublished report). These were not included in the study because of their recent chronology into the early modern period and young age. Juveniles exhibit enriched $\delta^{13}C$ and $\delta^{15}N$ values relative to adults, due to trophic effects from gestation and nursing 54,55 . Children also tend to eat different foods than adults 56 .

An individual recovered from an 8^{th} - 10^{th} c. kurgan-style burial was included in this study. The low-lying stone mound was located seven meters from the cluster of early modern burials. A looted context was found that contained disarticulated remains of a female individual (KZ-BR5), which was directly dated to cal AD 773-916 (OS-72514 1160 \pm 30 BP), which is first reported here. The other two medieval individuals that were included in this study were excavated in 2006. Two individuals (Karatal BR-1 and BR-2) were excavated after discovering the remains were partially exposed and threatened by an advancing erosional cut in the topsoil and deeper strata. Karatal BR-2 was directly radiocarbon dated to cal AD 972- 1032^{57} , and Karatal BR-1 is presumed to be from the same period based on stratigraphic positioning and associated horse riding tack and iron weapons, similar to those found in burials in the medieval period 51 . Around one of the leg bones of the Karatal BR-2 individual, the excavators found a cooper band that had preserved two small pieces of woven cotton 57 .

The finding of cotton fabrics suggests that cotton may have been an exchange good along the Silk Roads during the 10th-11th c., as it is possible that cotton could not have been grown as far north as Zhetysu⁵⁷. However, medieval agriculture in Zhetysu may have supported water demanding crops such as cotton, on account of rice being grown to this day in the Karatal River watershed⁵⁸ and rice grains were recovered from medieval sites in the Otrar Oasis²⁵. The only subsistence data recovered from excavated Karatal burials included a small number of sheep bones in KZ-BR5 that represent one individual animal, and a horse burial next to Karatal BR-1 that was not fully excavated.

Turkmenistan

Dehistan Plain

Geoktchik Depe is an urban complex of approximately 5.5 hectares that comprises two main features: a large mound that contains much of the Iron Age occupation (13th-8th c. BC) and a rectangular structure that is associated with the Sassanid and Islamic period (6th-16th c.)⁵⁹. The site contains a rich faunal assemblage, which has been published in detail, and suggests a strong pastoral component to subsistence⁵⁹. Notably, a small number of fish and bird bones were recovered from several phases of the site⁵⁹, which had been incorrectly reported in a paleodietary study presenting a stable isotope analysis⁶⁰. The site is associated with a complex network of irrigation canals that likely supported intensive farming⁵⁹, which appears to have been dominated by C₃ crops (wheat and barley) that primarily contributed to human diets at the site⁶⁰.

Misrijan is not well described in the English archaeological literature beyond a mention of being a "medieval town"⁵⁹, and a search for specific information about the site was unsuccessful. Human and fauna carbon and nitrogen isotopic values are reported from the site, but cultural details are not provided⁶⁰. There is a detailed monograph in Russian that describes the medieval archaeological sites on the Dehistan Plain⁶¹. However, the naming of the site under analysis as "Misrijan" by Bocherens et al.⁶⁰ may be confused with the Misrijan Oasis, which contains dozens of large medieval settlements and precludes identifying the precise site at this time.

Supplementary Table S1: Raw isotope data and information on human samples from medieval sites in Uzbekistan and Kazakhstan that were newly analysed in this study.

Separat Sepa	Lab ID	Archival ID	Original ID	Region	Site	Chronology	Skeletal element	Portion	Side	Sex	Age (years)	δ ¹³ C (‰)	δ ¹⁵ N (‰)	C:N	%C	%N
4			· ·	-		-										
497 497 497 292 597 697		·		,			·	,			, ,					
4491 4Sprack 6 21/10 Ferghana Valley Chartok 12h c. medial surface left Male Middle Aduit (35-50) 16.8 11.24 3.31 48.93 16.88 14.94 49.73 15.98 15.98 11.24 3.31 48.93 16.83 18.93 48.93 18.83 48.93 18.93 48.93 18.93 48.93 18.93 48.93 18.93 48.93 18.93 48.93 48.93 18.93 48.93 18.93 48.93 <td></td> <td>•</td> <td></td> <td></td> <td></td> <td></td> <td>·</td> <td>,</td> <td></td> <td></td> <td>o (,</td> <td></td> <td></td> <td></td> <td></td> <td></td>		•					·	,			o (,					
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Agrant 1 18ga Ferghana Valley Chartok 12la C		·		,							, ,					
4911 Pagnax 17 187 Ferghana Valley Charlok 12th c. parietal superior of eminence left Female Old Adult (50+) 1.6.68 1.1.2 3.27 48.28 18.89 4952 Чартах 167 Ferghana Valley Charlok 12th c. parietal superior of eminence left Unknown Old Adult (30+0) 1.5.0 1.07 3.24 46.95 16.89 4953 Чартах 12th Perghana Valley Charlok 12th c. parietal superior of eminence left Mole? Voung/Middle Adult (18-40) 1.5.52 10.59 3.20 46.95 16.79 4956 HQL4 11.401, 1.19 Ferghana Valley Chor Dona 11th 13th c. mandible medial surface left Male Young/Middle Adult (30-50) 17.17 10.55 3.0 46.79 46.78 4956 HQL5 14-05, n.14 Ferghana Valley Chor Dona 11th 13th c. mandible medial surface right Male Adult		•						•			, ,					
4952 Vagrax3 16? Ferghana Valley Chatok 12lh c. parietal superior of eminence left Unknown Old Adult (50+) -16.10 10.77 3.24 46.95 16.75 4953 Vagrax1 12ga Ferghana Valley Charlok 12lh c. parietal superior of eminence left Female Middle/Old Adult (38-60+) -15.53 11.27 3.25 46.66 16.75 4954 Vagrax14 20ga Ferghana Valley Charlok 12lh c. parietal superior of eminence left Unknown Old Adult (30-60+) -15.52 10.59 3.26 46.95 16.97 4955 Vagrax11 11.ga Ferghana Valley Chor Dona 11b-13th.c. mandible medial surface left Unknown Old Adult (30-50) -16.97 10.85 3.26 46.99 16.60 4956 VQB 14-05, n.14 Ferghana Valley Chor Dona 11b-13th.c. medial surface right Male Adult 16.57 18.		·		,			•	•	-		, ,					
Agrant 12µB Ferghana Valley Chartok 12h c. parietal superior of eminence left Female Middle/Old Adult (28-50+) -15.53 1.127 3.25 46.66 16.79				,			·				,					
Agraka14 20,000 Ferghana Valley Chartok 12th c. parietal Superior of eminence left Male? Young/Middle Adult (18-44) -15.52 10.59 3.26 46.95 16.79 Agraka14 11,000 Ferghana Valley Chartok 12th c. parietal Superior of eminence left Unknown Old Adult (50+) -17.17 10.55 3.30 46.06 18.47 Agraka14 14-01 n.19 Ferghana Valley Chor Dona 11th-13th c. mandible medial surface left Male Young/Middle Adult (30-50) -16.07 10.85 3.26 46.95 16.76 Agraka14 14-01 n.19 Ferghana Valley Chor Dona 11th-13th c. mandible medial surface right Male Adult Middle Adult (30-50) -17.10 9.91 3.33 3.05 16.70 Agraka14 14-06 n.17 Ferghana Valley Chor Dona 11th-13th c. mandible medial surface right Male Adult -18.33 10.09 3.26 45.95 16.39 Agraka14 14-06 n.17 Ferghana Valley Chor Dona 11th-13th c. temporal zygomatic arch right Male Adult -18.33 10.91 3.31 3.15 45.20 16.39 Agraka14				,			·	,			, ,					
4955 Vaprak11 11дв Ferghana Valley Chartok 12th c. parietal superior of eminence left Unknown Old Adult (50+) -17.17 10.55 3.30 46.60 16.76 4956 VДА 14-01, n.19 Ferghana Valley Chor Dona 11th-13th c. mandible medial surface left Male Middle Adult (30-50) -16.97 10.85 3.20 46.79 16.76 4958 VДБ 14-05, n.14 Ferghana Valley Chor Dona 11th-13th c. mandible medial surface right Male Adult -18.33 10.09 3.22 45.20 16.39 4950 VДД 14-06, n.17 Ferghana Valley Chor Dona 11th-13th c. temporal zygomatic arch right Male Adult -16.68 11.71 3.15 44.35 16.44 4961 TBK J6 BR2 Indiv. 1 TBK J6 BR2 Indiv. 1 West Pamir-Alay 7ashbulak 10th-11th c. tibla medial proximal shaft right Middle/Old Adult (30-50+ <t< td=""><td></td><td>•</td><td></td><td>,</td><td></td><td></td><td>·</td><td>,</td><td></td><td></td><td>, ,</td><td></td><td></td><td></td><td></td><td></td></t<>		•		,			·	,			, ,					
4956 ЧД4 14-01, n.19 Ferghana Valley Chor Dona 11th-13th c. mandible medial surface left Male Young/Middle Adult (23-50) -16.97 10.85 3.26 46.79 16.76 49.58 ЧД5 14-05, n.14 Ferghana Valley Chor Dona 11th-13th c. mandible medial surface right Male Middle Adult (30-50) -17.10 9.91 3.33 46.59 16.33 49.59 ЧД3 14-06, n.17 Ferghana Valley Chor Dona 11th-13th c. mandible medial surface right Male Adult 30-50) -17.10 9.91 3.33 46.59 16.39 49.59 ЧД3 14-06, n.17 Ferghana Valley Chor Dona 11th-13th c. temporal zygomatic arch right Male Adult 30-50) -16.68 11.71 3.15 44.35 16.44 49.61 ТВК Ј6 ВR2 Indiv. 1 ТВК Ј6 ВR3 Indiv. 1 ТВК Б6 ВR4 Indiv. 1 ТВК Б6 ВR4 Indiv. 1 ТВК Б6 ВR5 Indiv. 1 ТВК Б		·		,			•	•			, ,					
4958 ЧД5 14-05, п.14 Ferghana Valley Chor Dona 11th-13th c. mandible medial surface right Male Middle Adult (30-50) -17.10 9.91 3.33 46.56 16.33 4959 ЧД3 14-06, п.17 Ferghana Valley Chor Dona 11th-13th c. temporal zygomatic arch right Male Adult -18.33 10.09 3.22 45.20 16.39 4960 ЧД1 14-06 Ferghana Valley Chor Dona 11th-13th c. temporal zygomatic arch right Male Adult -16.68 11.71 3.15 44.35 16.44 4961 TBK J6 BR2 Indiv. 1 TBK J6 BR2 Indiv. 1 TBK F6 BR4 Indiv. 1 West Pamir-Alay Tashbulak 10th-11th c. tibia medial proximal shaft right Female Middle/Old Adult (30-50+) -18.34 10.07 3.14 44.34 16.47 4963 TBK F6 BR5 Indiv. 1 TBK F6 BR5 Indiv. 1 TBK F6 BR5 Indiv. 1 West Pamir-Alay Tashbulak 10th-11th c. tibia		·						•			,					
4959 ЧДЗ 14-06, п.17 Ferghana Valley Chor Dona 11th-13th c. mandible medial surface right Male Adult -18.33 10.09 3.22 45.20 16.39 4960 ЧД1 14-06 Ferghana Valley Chor Dona 11th-13th c. temporal zygomatic arch right Male Adult -16.68 11.71 3.15 44.35 16.44 4961 TBK J6 BR2 Indiv. 1 TBK J6 BR2 Indiv. 1 West Pamir-Alay Tashbulak 10th-11th c. tibia medial proximal shaft right Female Voung/Middle Adult (30-50+) -18.34 10.07 3.14 44.34 16.47 14.96 TBK J6 BR3 Indiv. 1 TBK J6 BR3 Indiv. 1 TBK J6 BR3 Indiv. 1 West Pamir-Alay Tashbulak 10th-11th c. tibia medial proximal shaft right Female Voung/Middle Adult (30-50+) -17.54 9.33 3.10 45.70 17.21 14.96 TBK J6 BR3 Indiv. 1 West Pamir-Alay Tashbulak 10th-11th c. tibia medial proximal shaft right Female Voung/Middle Adult (30-50+) -17.54 9.33 3.10 45.70 17.21 14.96 TBK J6 BR3 Indiv. 1 TBK J6 BR3 Indiv. 1 West Pamir-Alay Tashbulak 10th-11th c. tibia medial proximal shaft right Female Voung/Middle Adult (30-50+) -17.54 9.33 3.10 45.70 17.21 14.96 TBK J6 BR3 Indiv. 1 TBK J6 BR3 Indiv. 1 West Pamir-Alay Tashbulak 10th-11th c. tibia medial proximal shaft right Female Voung/Middle Adult (30-50+) -17.54 9.33 3.10 45.70 17.21 14.96 TBK J6 BR3 Indiv. 1 West Pamir-Alay Frinkent 10th-13th c. parietal superior of eminence right Male Middle/Old Adult (30-50+) -17.61 11.20 3.19 45.69 16.69 16.69 17.60	4956	ЧД4	14-01, п.19	Ferghana Valley	Chor Dona	11th-13th c.	mandible	medial surface	left	Male	Young/Middle Adult (23-50)	-16.97	10.85	3.26	46.79	
4960 ЧД1 14-06 Ferghana Valley Chor Dona 11th-13th c. temporal zygomatic arch right Male Adult —16.68 11.71 3.15 44.35 16.44 14.64 17.85	4958	ЧД5	14-05, п.14	Ferghana Valley	Chor Dona	11th-13th c.	mandible	medial surface	right	Male	Middle Adult (30-50)	-17.10	9.91	3.33	46.56	16.33
1. 1 TBK J6 BR2 Indiv. 1 TBK J6 BR2 Indiv. 1 TBK J6 BR2 Indiv. 1 TBK F6 BR4 Indiv. 1 TBK F6 BR4 Indiv. 1 West Pamir-Alay Tashbulak 10th-11th c. tibia medial proximal shaft right Female Middle/Old Adult (30-50+) -18.34 10.07 3.14 44.34 16.47 16.4	4959	ЧД3	14-06, п.17	Ferghana Valley	Chor Dona	11th-13th c.	mandible	medial surface	right	Male	Adult	-18.33	10.09	3.22	45.20	16.39
4962 ТВК F6 BR4 Indiv. 1 ТВК F6 BR4 Indiv. 1 ТВК F6 BR4 Indiv. 1 West Pamir-Alay Tashbulak 10th-11th c. tibia medial proximal shaft right Female Young/Middle Adult (30-50+) -17.54 9.33 3.10 45.70 17.21 17.21 17.54 17.54 9.33 3.10 45.70 17.21 17.21 17.54 17.	4960	ЧД1	14-06	Ferghana Valley	Chor Dona	11th-13th c.	temporal	zygomatic arch	right	Male	Adult	-16.68	11.71	3.15	44.35	16.44
4963 TBK F6 BR5 Indiv. 1 TBK F6 BR5 Indiv. 1 West Pamir-Alay Tashbulak 10th-11th с. tibia medial proximal shaft right Female Young/Middle Adult (27-50) -17.54 9.33 3.10 45.70 17.21 4964 TBK J6 BR1 Indiv. 1 TBK J6 BR1 Indiv. 1 West Pamir-Alay Tashbulak 10th-11th с. tibia medial proximal shaft right Female Old Adult (50+) -17.90 9.54 3.18 46.13 16.91 4965 Фринкент N1 West Pamir-Alay Frinkent 10th-13th с. parietal superior of eminence right Male Middle/Old Adult (30-50+) -19.02 11.92 3.18 43.00 15.87 4966 Фринкент N5 West Pamir-Alay Frinkent 10th-13th с. parietal superior of eminence left Female Old Adult (50+) -17.61 11.20 3.19 45.69 16.69 4968 Фринкент N5 West Pamir-Alay Frinkent 10th-13th с. parietal superior of eminence left Female Middle/Old Adult (30-50+) -18.66 11.43 3.23 45.88 16.56 4968 Фринкент N3 West Pamir-Alay Frinkent 10th-13th с. parietal superior of eminence right Male Middle/Old Adult (30-50+) -17.38 11.17 3.31 48.45 17.09	4961	TBK J6 BR2 Indiv. 1	TBK J6 BR2 Indiv. 1	West Pamir-Alay	Tashbulak	10th-11th c.	tibia	medial proximal shaft	left	Female	Young/Middle Adult (27-50)	-19.08	10.93	3.15	46.43	17.18
4964 ТВК J6 BR1 Indiv. 1 ТВК J6 BR1 Indiv. 1 ТВК J6 BR1 Indiv. 1 West Pamir-Alay Tashbulak 10th-11th с. tibia medial proximal shaft right Female Old Adult (50+) -17.90 9.54 3.18 46.13 16.91 4965 Фринкент4 N1 West Pamir-Alay Frinkent 10th-13th с. parietal superior of eminence right Male Middle/Old Adult (30-50+) -19.02 11.92 3.18 43.30 15.87 4966 Фринкент5 N2 West Pamir-Alay Frinkent 10th-13th с. parietal superior of eminence left Female Old Adult (50+) -17.61 11.20 3.19 45.69 16.69 4967 Фринкент3 N5 West Pamir-Alay Frinkent 10th-13th с. parietal superior of eminence left Female Middle/Old Adult (30-50+) -18.66 11.43 3.23 45.88 16.56 4968 Фринкент1 N3 West Pamir-Alay Frinkent 10th-13th с. parietal superior of eminence right Male Middle/Old Adult (30-50+) -17.38 11.17 3.31 48.45 17.09	4962	TBK F6 BR4 Indiv. 1	TBK F6 BR4 Indiv. 1	West Pamir-Alay	Tashbulak	10th-11th c.	tibia	medial proximal shaft	right	Female	Middle/Old Adult (30-50+)	-18.34	10.07	3.14	44.34	16.47
4965 Фринкент4 N1 West Pamir-Alay Frinkent 10th-13th c. parietal superior of eminence right Male Middle/Old Adult (30-50+) -19.02 11.92 3.18 43.30 15.87 4966 Фринкент5 N2 West Pamir-Alay Frinkent 10th-13th c. parietal superior of eminence left Female Old Adult (50+) -17.61 11.20 3.19 45.69 16.69 4967 Фринкент3 N5 West Pamir-Alay Frinkent 10th-13th c. parietal superior of eminence left Female Middle/Old Adult (30-50+) -18.66 11.43 3.23 45.88 16.56 4968 Фринкент1 N3 West Pamir-Alay Frinkent 10th-13th c. parietal superior of eminence right Male Middle/Old Adult (30-50+) -17.38 11.17 3.31 48.45 17.09	4963	TBK F6 BR5 Indiv. 1	TBK F6 BR5 Indiv. 1	West Pamir-Alay	Tashbulak	10th-11th c.	tibia	medial proximal shaft	right	Female	Young/Middle Adult (27-50)	-17.54	9.33	3.10	45.70	17.21
4966 Фринкент5 N2 West Pamir-Alay Frinkent 10th-13th c. parietal superior of eminence left Female Old Adult (50+) -17.61 11.20 3.19 45.69 16.69 4967 Фринкент3 N5 West Pamir-Alay Frinkent 10th-13th c. parietal superior of eminence left Female Middle/Old Adult (30-50+) -18.66 11.43 3.23 45.88 16.56 4968 Фринкент1 N3 West Pamir-Alay Frinkent 10th-13th c. parietal superior of eminence right Male Middle/Old Adult (30-50+) -17.38 11.17 3.31 48.45 17.09	4964	TBK J6 BR1 Indiv. 1	TBK J6 BR1 Indiv. 1	West Pamir-Alay	Tashbulak	10th-11th c.	tibia	medial proximal shaft	right	Female	Old Adult (50+)	-17.90	9.54	3.18	46.13	16.91
4967 Фринкент3 N5 West Pamir-Alay Frinkent 10th-13th c. parietal superior of eminence left Female Middle/Old Adult (30-50+) -18.66 11.43 3.23 45.88 16.56 14.968 Фринкент1 N3 West Pamir-Alay Frinkent 10th-13th c. parietal superior of eminence right Male Middle/Old Adult (30-50+) -17.38 11.17 3.31 48.45 17.09	4965	Фринкент4	N1	West Pamir-Alay	Frinkent	10th-13th c.	parietal	superior of eminence	right	Male	Middle/Old Adult (30-50+)	-19.02	11.92	3.18	43.30	15.87
4968 Фринкент1 N3 West Pamir-Alay Frinkent 10th-13th c. parietal superior of eminence right Male Middle/Old Adult (30-50+) -17.38 11.17 3.31 48.45 17.09	4966	Фринкент5	N2	West Pamir-Alay	Frinkent	10th-13th c.	parietal	superior of eminence	left	Female	Old Adult (50+)	-17.61	11.20	3.19	45.69	16.69
	4967	Фринкент3	N5	West Pamir-Alay	Frinkent	10th-13th c.	parietal	superior of eminence	left	Female	Middle/Old Adult (30-50+)	-18.66	11.43	3.23	45.88	16.56
4970 Алтун1 03-85, N2 West Pamir-Alay Altyntepe 10th-13th c. parietal superior of eminence right Male? Middle Adult (30-50) -17.56 9.14 3.32 46.54 16.34	4968	Фринкент1	N3	West Pamir-Alay	Frinkent	10th-13th c.	parietal	superior of eminence	right	Male	Middle/Old Adult (30-50+)	-17.38	11.17	3.31	48.45	17.09
	4970	Алтун1	03-85, N2	West Pamir-Alay	Altyntepe	10th-13th c.	parietal	superior of eminence	right	Male?	Middle Adult (30-50)	-17.56	9.14	3.32	46.54	16.34
4971 YT8 п.37 Tashkent Oasis Uturlik Tepe 10th-12th c. parietal superior of eminence right Unknown Unknown -16.82 13.29 3.39 47.05 16.17	4971	УТ8	п.37	Tashkent Oasis	Uturlik Tepe	10th-12th c.	parietal	superior of eminence	right	Unknown	Unknown	-16.82	13.29	3.39	47.05	16.17

Supplementary Information 10

Supplementary Table S1: Raw isotope data and information on human samples from medieval sites in Uzbekistan and Kazakhstan that were newly analysed in this study.

4972	УТ1	п.22	Tashkent Oasis	Uturlik Tepe	10th-12th c.	mandible	medial surface	right	Male	Old Adult (50+)	-17.11	12.56	3.30	46.49	16.43
4973	УТ3	п.45	Tashkent Oasis	Uturlik Tepe	10th-12th c.	mandible	medial surface	right	Female?	Adult	-18.16	11.85	3.31	46.50	16.40
4974	УТ2	71, холма	Tashkent Oasis	Uturlik Tepe	10th-12th c.	temporal	zygomatic arch	right	Male?	Young/Middle Adult (18-44)	-18.22	12.51	3.27	47.50	16.96
4975	УТ7	п.39	Tashkent Oasis	Uturlik Tepe	10th-12th c.	mandible	inferior of body	right	Unknown	Unknown	-16.02	13.89	3.35	48.80	16.99
4976	УТ5	п.35	Tashkent Oasis	Uturlik Tepe	10th-12th c.	mandible	medial surface	right	Male	Young Adult (18-30)	-17.19	13.50	3.35	47.72	16.64
4977	УТ6	п.15	Tashkent Oasis	Uturlik Tepe	10th-12th c.	parietal	superior of eminence	right	Unknown	Unknown	-17.07	12.05	3.34	47.44	16.57
4978	УТ4	п.46	Tashkent Oasis	Uturlik Tepe	10th-12th c.	parietal	superior of eminence	right	Male	Middle/Old Adult (30-50+)	-18.03	12.70	3.32	46.81	16.47
4979	УТ9	п.46	Tashkent Oasis	Uturlik Tepe	10th-12th c.	mandible	inferior of body	right	Unknown	Unknown	-18.71	12.64	3.17	44.91	16.51
4980	TK12	п.15,N11	Khoresm	Tok Kala	9th-11th c.	parietal	superior of eminence	left	Female	Middle Adult (30-50)	-13.07	13.32	3.32	48.46	17.02
4982	TK15	п.40,N26	Khoresm	Tok Kala	9th-11th c.	parietal	superior of eminence	left	Male	Young/Middle Adult (18-44)	-12.71	11.57	3.22	46.82	16.95
4983	TK18	п.5,N25	Khoresm	Tok Kala	9th-11th c.	parietal	superior of eminence	left	Male?	Middle Adult (30-50)	-12.61	12.48	3.28	46.83	16.64
4984	TK5	п.20,N14	Khoresm	Tok Kala	9th-11th c.	parietal	superior of eminence	right	Male?	Middle Adult (30-50)	-15.11	13.99	3.33	48.33	16.92
4985	TK9	п.32,N31	Khoresm	Tok Kala	9th-11th c.	parietal	superior of eminence	left	Female?	Middle Adult (30-50)	-14.36	13.38	3.30	47.20	16.67
4986	TK23	п.15,N8	Khoresm	Tok Kala	9th-11th c.	parietal	superior of eminence	left	Male	Middle/Old Adult (30-50+)	-13.00	13.01	3.31	48.61	17.15
4987	Tk20	п.22,N3	Khoresm	Tok Kala	9th-11th c.	parietal	superior of eminence	left	Female?	Young Adult (20-30)	-13.30	12.53	3.29	47.78	16.93
4988	TK13	п.29,N9	Khoresm	Tok Kala	9th-11th c.	parietal	superior of eminence	left	Male?	Middle Adult (30-50)	-12.40	12.40	3.29	48.24	17.09
4989	TK1	п.8	Khoresm	Tok Kala	9th-11th c.	parietal	superior of eminence	left	Male	Old Adult (50+)	-13.52	12.59	3.30	45.94	16.26
6965	Karatal BR-2	Karatal BR-2	Zhetysu	Karatal	10th-11th c.	mandible	inferior of body	right	Unknown	Adult	-18.11	12.65	2.94	43.49	17.27
6966	Karatal BR-1	Karatal BR-1	Zhetysu	Karatal	10th-11th c.	tibia	medial proximal shaft	left	Male	Middle Adult (35-49)	-17.98	13.86	3.13	45.93	17.15
5164	KZ-BR5	KZ-BR5	Zhetysu	Karatal	8th-10th c.	femur	medial proximal shaft	right	Female	Middle Adult (35-49)	-16.20	12.39	3.10	45.49	17.07

Carbon isotope reference:

VPDE

Nitrogen isotope reference:

AIR

Supplementary Information 11

Supplementary Table S2: Raw isotope data of medieval human from southeastern Kazakhstan previously published in Motuzaite Matuzeviciute et al.⁴³

Lab ID	Original ID	Region	Site	Chronology	δ ¹³ C (‰)	δ ¹⁵ N (‰)	C:N
GM_139	Kurgan 1/grave 17	Otrar Oasis	Konyr-Tobe I	5th-7th c.	-15.3	12.7	3.33
GM_141	Kurgan 1/grave 15	Otrar Oasis	Konyr-Tobe I	5th-7th c.	-13.8	11.5	3.07
GM_142	Kurgan 1/grave16	Otrar Oasis	Konyr-Tobe I	5th-7th c.	-12.4	12.9	3.32
GM_145		Otrar Oasis	Konyr-Tobe I	5th-7th c.	-19.1	12.1	3.08
GM_146	Kurgan 1/grave 13	Otrar Oasis	Konyr-Tobe I	5th-7th c.	-18.2	10.7	3.11
GM_144	Kurgan 1/grave 6	Otrar Oasis	Konyr-Tobe I	5th-7th c.	-17.4	11.1	3.32
GM_147	Kurgan 1/grave 17	Otrar Oasis	Konyr-Tobe I	5th-7th c.	-16.8	12.1	3.09
GM_143		Otrar Oasis	Konyr-Tobe I	5th-7th c.	-18.7	12.8	3.09
GM_140	Kurgan 1/grave 14	Otrar Oasis	Konyr-Tobe I	5th-7th c.	-18.6	11.9	3.11
GM_001	Kurgan 20	Otrar Oasis	Temirlanovka	2nd-4th c.	-13.65	13.20	3.26
GM_002	Kurgan 26	Otrar Oasis	Temirlanovka	2nd-4th c.	-12.60	12.01	3.23
GM_005	Kurgan 33/grave 1	Otrar Oasis	Temirlanovka	2nd-4th c.	-13.18	13.18	3.19
GM_004	Kurgan 33/grave 2	Otrar Oasis	Temirlanovka	2nd-4th c.	-14.59	13.98	3.18
GM_007	Kurgan 10/grave 1	Zhetysu	Turgen II	2nd-6th c.	-16.65	11.72	3.41
GM_013	Kurgan 7/grave 1	Zhetysu	Turgen II	2nd-6th c.	-17.26	10.97	3.15
GM_009	Kurgan 10/grave 3	Zhetysu	Turgen II	2nd-6th c.	-15.05	11.86	3.52
GM_010		Zhetysu	Turgen II	2nd-6th c.	-18.09	10.40	3.10
GM_008	Kurgan 10/grave 2	Zhetysu	Turgen II	2nd-6th c.	-15.46	11.69	3.44
GM_012	Kurgan 8	Zhetysu	Turgen II	2nd-6th c.	-15.20	11.43	3.10
GM_006	Kurgan 9	Zhetysu	Turgen II	2nd-6th c.	-15.55	11.76	3.52
GM_ 015	Grave 16	Zhetysu	Butakty I	10th-12th c.	-10.66	11.32	3.15
GM_016	Kurgan 35/2	Zhetysu	Butakty I	10th-12th c.	-11.18	12.12	3.40
GM_018	Grave 23	Zhetysu	Butakty I	10th-12th c.	-12.11	11.71	3.22
GM_017	Grave 35/1	Zhetysu	Butakty I	10th-12th c.	-11.17	12.16	3.13
GM_014	Kurgan 1/grave 1	Zhetysu	Butakty I	10th-12th c.	-15.34	10.71	3.22
GM_003		Zhetysu	Butakty I	10th-12th c.	-15.70	11.24	3.14

Notes:

Isotope values are rounded to the nearest hundredth, while data from Konyr-Tobe I are reported to the nearest tenth, as previously published.

Skeletal element data were not provided in original source.

Archaeological contextual information is transcribed as published and placed in the "Original ID" column here.

Original Western Arabic numerals after site names have been replaced here with Roman numerals.

%C and %N were not reported.

Supplementary Table S3: Raw isotope data of medieval and Iron Age human isotopic data from Turkmenistan previously published in Bocherens et al.⁶⁰

Sample ID	Region	Site	Chronology	Skeletal element	Age	δ ¹³ C (‰)	δ ¹⁵ N (‰)	C:N	%C	%N
MS 101	Dehistan	Misrijan	11th-12th c.	mandible	6/7 years	-19.5	14.8	3.2	45.0	16.5
GD 94/303	Dehistan	Geotchik Depe	Iron Age	mandible	adult	-20.1	14.2	3.2	25.9	9.3
GD 95/433	Dehistan	Geotchik Depe	Iron Age	talus	adult	-20.1	13.6	3.2	39.4	14.3

Supplementary Table S4: Rejected human samples from medieval sites in Uzbekistan

Lab											$\delta^{13}C$	$\delta^{15}N$				
ID	Archival ID	Original ID	Region	Site	Chronology	Skeletal element	Portion	Sex	Age (years)	Side	(‰)	(‰)	C:N	%C	%N	Comment
											-					
4957	ЧД2	14-07, п.16	Ferghana Valley	Chor Dona	11th-13th c.	mandible	medial surface	Male?	Young/Middle Adult (20-43)	right	21.43	9.84	5.13	52.64	11.97	Excess carbon
4969	Фринкент2	п.4	West Pamir-Alay	Frinkent	10th-13th c.	frontal	-	Female?	Young Adult (20-30)	right	-	-	-	-	-	Failed extraction
4981	TK19	п.37,N17	Khoresm	Tok Kala	9th-11th c.	parietal	superior of eminence	Female?	Young/Middle Adult (18-50)	left	-	-	-	-	-	Failed extraction

Carbon isotope reference: VPDB

Nitrogen isotope reference: AIR

Supplementary Information 4: $\delta^{13}C$ and $\delta^{15}N$ means and 95% CIs obtained from Bayesian bootstrapping (mean_b)

-16.98

-16.00

-20.16

-15.53

-12.56

-19.61

δ^{13} C mean _b			
Region	Mean	2.50%	97.50%
W_Pamir_Alay	-18.12	-18.53	-17.76
Ferghana	-16.28	-16.74	-15.88
Tashkent	-17.49	-17.97	-16.98
Khoresm	-13.34	-13.91	-12.90
Otrar_late	-16.71	-17.94	-15.15
Otrar_early	-13.51	-14.18	-12.92

-16.18

-14.27

-19.93

 $\delta^{15}N \; mean_b$

Zhetysu_early

Zhetysu_late

Dehistan

Region	Mean	2.50%	97.50%
W_Pamir_Alay	10.53	9.94	11.10
Ferghana	10.80	10.53	11.05
Tashkent	12.78	12.40	13.18
Khoresm	12.81	12.39	13.23
Otrar_late	11.98	11.50	12.41
Otrar_early	13.09	12.44	13.66
Zhetysu_early	11.40	11.01	11.67
Zhetysu_late	12.01	11.50	12.60
Dehisan	14.20	13.73	14.67

Supplementary Information 5: Environmental modelling

Environmental conditions at sites were estimated from abiotic variables using an approach combining geographic information system (GIS) and redundancy analysis (RDA). Both 10 and 50 km analytical buffers were created around each site, which was used to calculate two sets of spatial means of various climatic and soil parameters derived from geographic data layers (Supplemental Tables S5-S6). Supplemental Fig. S1 shows examples of annual mean temperature, precipitation of wettest and driest month, and weight % of clay in soil. Climatic data were obtained from the WorldClim project (http://worldclim.org/), which describe biologically meaningful variations of temperature and precipitation in ca. 1 km resolution (bioclim)⁶². These data represent monthly climate records from 1970-2000. This period is similar in average temperature and precipitation to the 'Medieval Warm Period' during the 8th-13th c. in Central Asia⁶³⁻⁶⁵. However, the early medieval period (2nd-6th c.), which is chronologically represented in our dataset, coincides with the 'Dark Ages Cold Period' and is less comparable to modern environmental patterns⁶⁶. Soil data were obtained from the Soil Grid project (http://isric.org/) to provide additional variables relevant for agricultural production⁶⁷. The size of the buffers serves three purposes: 1) represent two spatial scales of human life experiences, either through direct movement and interaction or through contact with others living in this zone; 2) capture environmental variation in site environs caused by landscape fluctuations, such as mountains acting as rain shields and having steep, rocky terrain that changes over short distances, which was especially evident for areas near Tashbulak, Butakty, and Turgen; 3) overcome differences in spatial scales of the underlying geographic data.

Environmental parameters for each site buffer where associated with that site's $\delta^{13}C$ and $\delta^{15}N$ mean, min, and max values. The mean isotope values, as point estimates, were insufficient to represent sites expressing wide isotopic variation, such as Konyr-Tobe in $\delta^{13}C$ or Temirlanovka in $\delta^{15}N$; min and max values were included to consider values at the ends of wide isotopic distributions, which were used in RDA with the R package vegan⁶⁸. In order to reduce the susceptibility of the RDA to false positives, statistical significance was set at p < 0.01. It is important to note that this figure is considered liberal by scientists from multiple fields, who recommend p < 0.005^{69} . Environmental parameters were examined for correlation and plotted as a distance matrix using hierarchical clustering (Supplemental Fig. S2). Highly correlated parameters were removed, and the remaining parameters were accepted to be used in RDA:

<u>50km</u>
elevation
bio1
bio2
bio3
bio4
bio15
CECSOL
CLYPPT

Using these parameters, stable isotopic data were fitted to each RDA using the envfit() function in vegan. No statistical significant relationships were found at p < 0.01. However, for the 10km dataset at p < 0.05 a negative correlation was found between mean δ^{13} C values and bio3 (isothermality), in addition to a positive correlation was found with bio4

(temperature seasonality). For the 50km dataset, a negative correlation was also found between accepted environmental parameters and bio3.

To further explore possible relationships, multiple linear regressions were performed using stable isotopic data and accepted environmental parameters. Critically, the Bonferroni correction was applied to the level of significance in order to counteract the problem of conducting multiple, simultaneous statistical tests, which would otherwise increase the probability of finding an erroneous result⁷⁰. An initial alpha value of 0.01 was divided by 8, representing the number of accepted environmental parameters, to get a new level of statistical significance of 0.00125. At this level, no linear relationships were identified. However, for accepted environmental datasets of both 10km and 50km, linear relationships were identified at uncorrected levels of significance. The strongest of these linear relationships were between mean δ^{13} C values and 10 km bio3 (slope = -0.57; R^2 = 0.483; p = 0.006) and mean δ^{15} N values and 10km elevation (slope = -0.002; R^2 = 0.325; p = 0.033), which are displayed in Supplemental Fig. S4.

Isothermality is a measure of the difference between day-to-night temperatures relative to the annual summer-to-winter temperatures. A value of 100 indicates that the diurnal temperature range is equal to the annual temperature range, and smaller values indicate lower temperature diurnal ranges against the annual range. C_4 plants, including millets used in agriculture, are well adapted to hot and arid climate⁷¹. Locations with lower isothermality values have higher human mean $\delta^{13}C$ values, but it is not clear why isothermality would correlate with human $\delta^{13}C$ values. The chances of this correlation being spurious is supported by a clustering of sites in the bi-plot in three groups along the trend line and an overall low range of isothermality values between ca. 27 and 35% (Supplemental Fig. S4), which suggests there is unlikely to be a dependent relationship with factors that would influence dietary intake of C_4 plants.

There also appears to be a weak, negative linear correlation between elevation and mean $\delta^{15}N$ values, but with a p-value of 0.033 and ca. 32.5% data explanation ($R^2 = 0.325$), confidence in this result should be checked. In hot and arid ecosystems, typical of lowland regions in Central Asia, plant $\delta^{15}N$ values increase due to nitrogen loss from soils⁷². Agricultural products in lowland zones, especially those downstream from further farming run-off, can also be enriched in ¹⁵N from exogenous inputs such as fertilizers and animal waste^{73–77}. Thus, it is not possible to separate these processes given the prevalence of highly modified agricultural landscapes in the medieval period of Central Asia. Furthermore, these results demonstrate that patterns of agricultural production and dietary intake are more likely to be minimally affected by inter-regional differences in environment that were modelled here.

Supplementary Table S5: 50 km environmental data used in regression and redundancy analysis that were derived from bioclimatic variables and soil properties.

site	elevation	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18	bio19	CECSOL	PHIHOX	ORCDRC	CLYPPT	SNDPPT
Altyntepe	496.7	15.3	14.7	35.4	971.7	35.8	-5.8	41.6	7.7	25.7	27.6	3.4	381.6	81.2	0.2	84.0	195.1	4.7	6.1	161.9	22.4	78.0	4.7	28.3	29.0
Butakty-2	1355.7	6.5	11.0	27.6	1078.1	25.7	-14.5	40.2	11.6	5.5	19.1	-7.3	427.0	68.7	16.3	47.8	177.6	56.7	114.7	61.0	24.8	70.9	17.5	27.9	28.4
Chartok	574.5	13.3	12.8	30.5	1023.4	32.7	-9.1	41.8	11.3	23.8	25.5	0.2	249.7	33.3	4.3	48.3	97.0	18.2	27.3	77.0	19.6	79.4	6.7	27.3	29.6
Chor Dona	564.0	13.5	12.7	29.9	1034.6	33.0	-9.4	42.3	8.4	24.1	25.8	0.1	269.5	35.5	5.1	47.7	101.9	19.5	27.0	87.7	18.9	77.8	9.3	29.3	27.2
Frinkent	580.7	13.9	14.1	34.3	973.6	33.7	-7.4	41.1	7.8	24.2	26.1	1.9	346.3	65.3	1.1	74.7	162.6	8.2	11.2	138.9	22.2	77.5	6.5	28.7	29.0
Geoktchik Depe	130.1	17.1	13.3	34.0	962.5	35.9	-3.1	39.0	12.2	28.8	28.8	5.3	194.2	32.3	4.1	54.7	78.4	15.1	15.1	65.6	17.2	81.1	2.5	22.2	39.6
Karatal	582.5	7.9	14.2	29.9	1222.7	30.6	-16.9	47.5	8.2	21.2	22.4	-7.7	332.9	38.5	14.0	28.9	105.8	56.3	69.4	73.2	28.1	78.0	9.5	28.8	27.7
Konyr-Tobe-1	182.7	12.8	14.4	30.9	1168.2	35.0	-11.6	46.6	5.1	25.2	27.2	-1.8	221.8	33.7	1.0	61.9	87.9	9.0	12.0	86.3	27.6	79.6	8.1	30.4	31.9
Misrijan	189.5	16.5	12.9	33.8	946.7	34.9	-3.1	38.0	13.4	28.1	28.1	4.9	195.8	32.0	4.4	54.3	79.8	16.1	16.1	65.3	17.6	80.9	3.1	24.7	35.5
Tashbulak	1872.2	8.5	12.3	33.6	879.4	26.7	-9.8	36.5	7.6	17.7	19.6	-2.1	406.2	74.0	7.5	61.2	194.2	35.4	51.4	99.4	25.2	71.0	15.1	28.0	33.7
Temirlanovka	318.8	13.2	14.9	32.8	1105.7	34.8	-10.6	45.4	6.9	25.1	26.8	-0.8	340.3	51.3	2.2	61.2	135.1	12.5	17.4	122.2	27.2	76.6	6.3	33.3	27.2
Tok Kala	62.5	11.8	12.4	27.7	1195.4	33.2	-11.6	44.8	12.7	24.0	26.3	-3.0	105.4	16.3	2.0	50.8	45.0	8.0	10.3	31.3	22.6	81.3	7.1	29.9	27.7
Turgen-2	1276.8	6.8	11.9	30.2	1029.0	26.1	-13.4	39.5	13.7	-5.4	19.0	-6.0	469.0	67.0	19.3	39.6	180.8	65.5	135.9	66.0	24.8	69.4	17.1	26.1	29.1
Uturlik	271.0	14.7	14.2	33.6	1006.3	34.9	-7.4	42.3	9.1	27.0	27.0	2.0	316.0	50.1	1.0	69.3	140.6	7.6	7.6	124.2	20.5	78.2	9.0	30.1	27.1

Supplemental Table S6: 10 km environmental data used in regression and redundancy analysis that were derived from bioclimatic variables 62 and soil properties 67.

Site	elevation	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18	bio19	CECSOL	PHIHOX	ORCDRD	CLYPPT	SNDPPT
Altyntepe	474.7	15.2	14.4	35.3	954.7	35.5	-5.2	40.7	7.4	25.4	27.3	3.6	380.8	81.2	0.0	84.0	194.3	4.6	6.0	162.3	20.1	77.8	6.0	27.9	29.5
Butakty-2	1154.0	7.7	10.7	26.4	1104.2	27.2	-13.4	40.6	14.2	1.8	20.5	-6.6	423.1	68.6	17.9	44.2	171.5	62.8	102.6	63.9	24.9	72.8	14.9	28.9	26.7
Chartok	544.7	13.5	12.7	30.3	1028.2	32.9	-9.1	42.0	11.5	23.9	25.7	0.2	240.5	32.0	3.9	48.2	92.3	16.7	25.6	75.5	18.4	79.3	6.5	26.6	30.7
Chor Dona	579.6	13.5	12.7	29.7	1038.2	33.3	-9.4	42.6	8.3	24.0	25.9	0.1	274.5	36.4	5.3	47.6	103.9	19.9	27.7	88.9	18.2	78.1	9.1	29.1	29.2
Frinkent	535.5	14.0	14.1	34.2	977.2	33.8	-7.4	41.2	8.2	24.3	26.2	1.9	341.4	64.9	1.0	75.5	161.1	7.5	10.2	138.0	21.0	78.1	6.4	28.5	28.3
Geoktchik Depe	127.1	17.2	13.3	33.8	966.1	36.2	-3.0	39.2	12.7	29.0	29.0	5.3	192.8	32.2	4.0	54.6	77.9	15.0	15.0	64.7	17.9	81.1	2.6	21.3	41.5
Karatal	621.2	8.0	14.0	30.4	1184.6	30.4	-15.8	46.2	7.6	21.1	22.1	-6.8	347.0	39.9	15.1	28.8	110.2	59.4	73.1	75.3	28.5	77.8	7.9	29.6	26.9
Konyr-Tobe-1	177.1	12.8	14.5	31.0	1168.1	35.0	-11.7	46.7	6.1	25.2	27.2	-1.8	222.5	33.5	1.0	61.5	87.3	9.0	12.0	86.4	27.9	79.8	9.0	30.7	31.2
Misrijan	168.3	16.3	12.7	33.6	945.1	34.7	-3.2	37.9	13.2	27.9	27.9	4.8	197.4	32.5	4.3	54.9	80.4	15.7	15.7	65.9	16.9	81.0	3.1	25.2	33.7
Tashbulak	1802.6	9.2	12.3	33.6	875.2	27.5	-9.0	36.5	8.6	19.2	20.2	-1.5	399.8	76.1	6.9	63.6	197.7	32.1	44.5	93.7	27.1	72.1	14.4	30.3	31.3
Temirlanovka	317.2	13.2	15.0	32.9	1105.8	35.0	-10.6	45.6	6.9	25.2	26.9	-0.7	340.9	51.6	2.0	61.2	135.3	12.2	17.3	122.1	27.2	76.5	5.4	33.5	26.6
Tok Kala	61.3	11.6	12.0	27.4	1182.4	32.7	-11.1	43.8	12.6	23.7	26.0	-2.9	103.8	15.8	2.0	50.3	44.1	8.0	10.3	31.1	23.8	81.5	6.5	30.0	27.5
Turgen-2	1041.4	8.2	11.7	29.3	1051.0	27.8	-12.1	39.8	14.4	-5.0	20.6	-5.0	456.5	65.9	20.2	37.1	173.1	67.8	118.5	67.8	24.7	70.6	17.7	28.0	26.1
Uturlik	270.0	14.7	14.3	33.9	1003.1	34.8	-7.3	42.1	9.1	27.0	27.0	2.0	315.3	49.8	1.0	69.4	140.5	7.5	7.5	123.9	20.3	78.6	10.7	30.5	26.4

Bioclimatic variables:

bio1 Annual mean temperature bio2 Annual mean diurnal range

bio3 Isothermality

bio4 Temperature seasonality (CV)

bio5 Max temperature of warmest month

bio6 Min temperature of coldest month

bio7 Annual temperature range

bio8 Mean temperature of wettest quarter

bio9 Mean temperature of driest quarter bio10 Mean temperature of warmest quarter

bio10 Mean temperature of warmest quarter bio11 Mean temperature of coldest quarter

bio12 Annual precipitation

bio13 Precipitation of wettest month

bio14 Precipitation of driest month

bio15 Precipitation seasonality (CV)

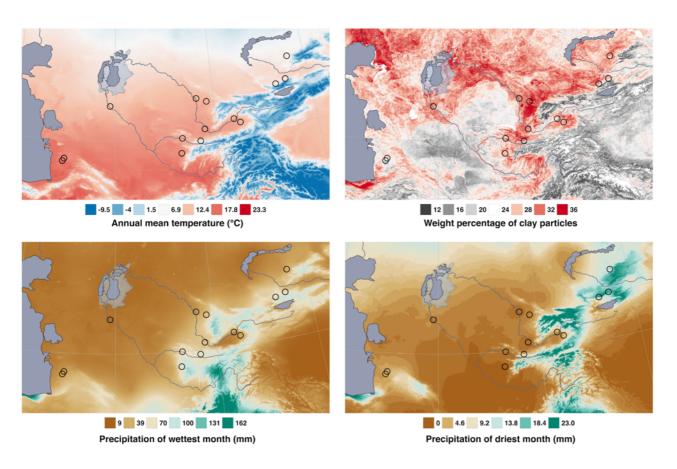
bio16 Precipitation of wettest quarter

bio17 Precipitation of driest quarter bio18 Precipitation of warmest quarter bio18 Precipitation of warmest quarter bio19 Precipitation of coldest quarter

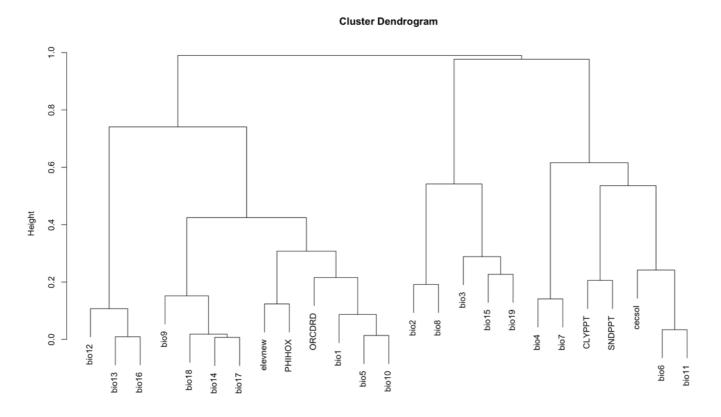
Soil properties:

CECSOL Cation exchange capacity
PHIHOX pH index in water solution
ORCDRC organic carbon content

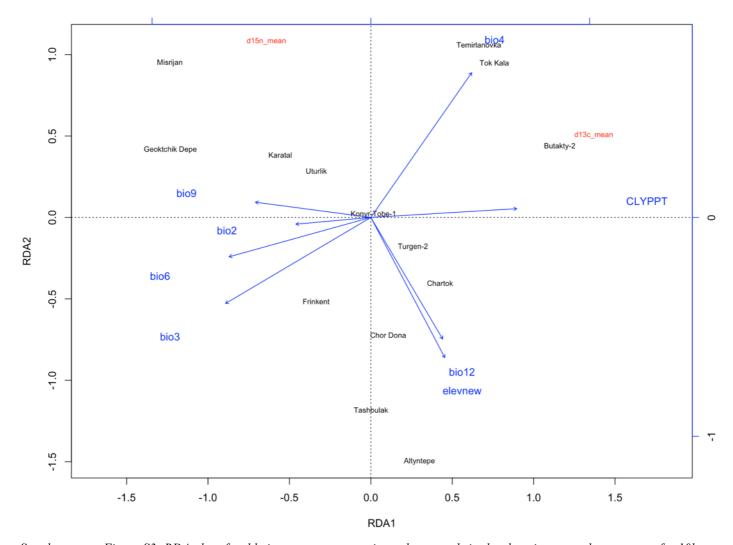
CLYPPT % wt clay particles (<0.0002 mm) SNDPPT % wt sand particles (0.05-2 mm



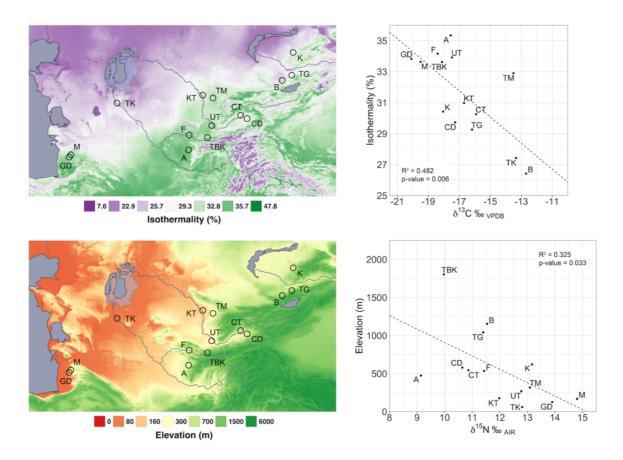
Supplementary Figure S1: Examples of geographic layers for environmental parameters and sites analysed in this study. Map scale and extent are identical to that in main text Fig. 1. Map generated with Quantum GIS, version 2.18.2 (https://www.qgis.org).



Supplementary Figure S2: Hierarchical clustering analysis of environmental variables derived from 10km buffers around sites.



Supplementary Figure S3: RDA plot of stable isotope means per site and accepted site-level environmental parameters for 10km buffers.



Supplementary Figure S4: Results of linear regression analysis between accepted environmental parameters and stable isotopic values. In the top panel, mean $\delta^{13}C$ values of each site moderately correlate with site isothermality (bio3). In the bottom panel, mean $\delta^{15}N$ values of each site weakly correlate with site elevation. The p-values here do not cross the level of significance after applying the Bonferroni correction. Site key: TK = Tok-kala, UT = Uturlik, CD = Chor Dona, CT = Chartok, TBK = Tashbulak, A = Altyntepe, F = Frinkent, GD = Geoktchik Depe, M = Misrijan, KT = Konyr-Tobe, TM = Temirlanovka, TG = Turgen, B = Butakty, K = Karatal. Map generated with Quantum GIS, version 2.18.2 (https://www.qgis.org).

Supplementary Information 6: Numerical output of isotopic niche modelling

SIBER Bayesian ellipse areas (‰²) that are depicted in main text Fig. 3:

Otrar (early)

Mode 1.2 Mean 2.04 Median 1.66

95 % lower = 0.441 upper = 4.5

75 % lower = 0.678 upper = 2.51

50 % lower = 0.863 upper = 1.84

Otrar (late)

Mode 4.91 Mean 6.21 Median 5.73

95 % lower = 2.66 upper = 10.8

75 % lower = 3.39 upper = 7.67

50 % lower = 3.95 upper = 6.37

Zhetysu (early)

Mode 1.19 Mean 1.56 Median 1.4

95 % lower = 0.575 upper = 2.89

75 % lower = 0.754 upper = 1.94

50 % lower = 0.899 upper = 1.56

Zhetysu (late)

Mode 7.26 Mean 9.04 Median 8.35

95 % lower = 3.87 upper = 15.7

75 % lower = 4.95 upper = 11.2

50 % lower = 5.77 upper = 9.3

Dehistan

Mode 0.425 Mean 0.839 Median 0.629

95 % lower = 0.13 upper = 2.05

75 % lower = 0.211 upper = 1

50 % lower = 0.282 upper = 0.693

Ferghana

Mode 1.4 Mean 1.57 Median 1.5

95 % lower = 0.846 upper = 2.44

75 % lower = 1.03 upper = 1.9

50 % lower = 1.15 upper = 1.65

Khoresm

Mode 1.28 Mean 1.59 Median 1.46

95 % lower = 0.68 upper = 2.76

75 % lower = 0.869 upper = 1.96

50 % lower = 1.01 upper = 1.63

Tashkent

Mode 1.34 Mean 1.67 Median 1.54

95 % lower = 0.713 upper = 2.9

75 % lower = 0.911 upper = 2.06

50 % lower = 1.06 upper = 1.71

West Pamir-Alay

Mode 1.71 Mean 2.13 Median 1.96

95 % lower = 0.91 upper = 3.7

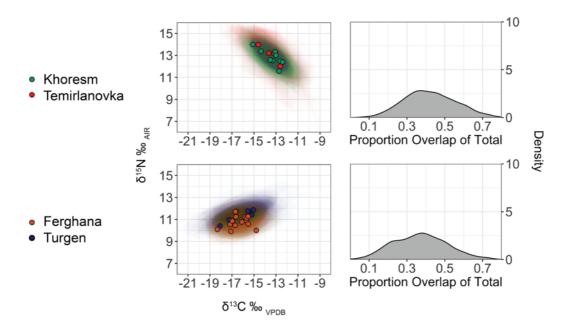
75 % lower = 1.16 upper = 2.63

50 % lower = 1.35 upper = 2.18

Supplementary Information 7: Isotopic niche overlap of urban medieval regions in Uzbekistan and Turkmenistan

SIBER Bayesian ellipse overlap analysis depicted in main text Figure 3, (Dehistan included below):

Regional pairs	Mean	Lower 95% CI	Upper 95% CI
West Pamir-Alay - Ferghana	18.8%	5.3%	35.5%
West Pamir-Alay - Tashkent	15.7%	3.2%	32.1%
West Pamir-Alay - Khoresm	0.0%	0.0%	0.0%
West Pamir-Alay - Dehistan	1.3%	0.0%	11.1%
Ferghana - Dehistan	0.0%	0.0%	0.0%
Ferghana - Khoresm	0.7%	0.0%	6.9%
Tashkent - Khoresm	2.2%	0.0%	12.9%
Tashkent - Ferghana	4.1%	0.0%	19.4%
Tashkent - Dehistan	1.1%	0.0%	11.7%
Khoresm - Dehistan	0.0%	0.0%	0.0%



Supplementary Figure S5: Isotopic niche overlap between Khoresm and Temirlanovka (early Otrar) (top) and between Ferghana and Turgen (early Zhetysu) (bottom).

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This manuscript is published as a chapter in *Isotopic Investigations of Pastoralism in Prehistory*. 2018. Edited by Alicia Ventresca-Miller and Cheryl Makarewicz. Routledge, London.

Ahead of the curve?

Implications for isolating vertical transhumance in seasonal montane environments using sequential oxygen isotope analyses of tooth enamel

TAYLOR HERMES, SARAH PEDERZANI, AND CHERYL A. MAKAREWICZ

Introduction

Vertical transhumance is a productive strategy used by pastoralists around the world. This type of mobility entails the movement of livestock to pastures located at different elevations, with moves calculated according to local, altitude-dependent availability of pasture growth, and provides a means of optimizing pastoral production to specific environmental conditions. Identification of the scheduled use of upland pastures offers a way to characterize subsistence economies and social interactions in pastoralist communities. Yet, directly establishing the scale of upland pasture use and, critically, the seasonality and duration of movements to spatially limited grassland resources remains challenging.

Stable isotope analysis, which directly measures dietary intake and environmental inputs recorded in plant and animal tissues (Ambrose and DeNiro, 1986; Koch et al., 1989; Krueger and Sullivan, 1984), offers a means to detect mobility to pastures in locations characterized by unique isotopic signatures. Recently, there has been a developing interest in the potential of using stable isotope analysis on domesticated-animal teeth as a way to isolate vertical transhumance in zooarchaeological assemblages associated with pastoral economies (Balasse and Ambrose, 2005; Henton, 2012; Henton et al., 2010; Mashkour, 2003; Mashkour et al., 2005). By exploiting the sensitivity of isotopic systems to the geospatial variation in vegetation, precipitation, and geological structure, it is possible to describe, at varying scales of resolution, the movements of animals across the landscape (Balasse et al., 2002; Bogaard et al., 2014; Hobson and Wassenaar, 2008; Julien et al., 2012; Makarewicz and Tuross, 2012; Stone, 2015).

Much research has inferred animal movements by comparing strontium isotope values measured from archaeological animal bone and teeth to ⁸⁷Sr/⁸⁶Sr values obtained from modern plants and animals collected from known locations presumed to represent a "baseline" of bioavailable strontium in past environments (Bogaard et al., 2014; Britton et al., 2011; Pellegrini et al., 2008; Sjögren and Price, 2013; Towers et al., 2011; Valenzuela-Lamas et al., n.d.). Outside of the many

methodological challenges in reconstructing bioavailable strontium in ancient environments (Bentley and Knipper, 2005; Price et al., 2002), the approach requires reconciliation between the degree of strontium isotopic variation in the geographic area of interest with the scale of movement under investigation. In cases where detection of vertical transhumance is desired, there is often a spatial mismatch between the distribution of biologically available strontium and patterns of animal mobility. In general, mountainous terrain is characterized by heterogeneous geological formations that impart high strontium-isotope variability that masks movements along elevation gradients spanning relatively small distances (e.g. Knudson et al., 2014). Using 87Sr/86Sr values in regions with steep land formations further complicates the isolation of mobility patterns, as a result of erosional processes that mix sediments derived from geological layers with various strontium isotopic ratios (Drake et al., 2014).

In order to reduce spatial insensitivity by relying on a single isotopic system, archaeologists have begun to pair strontium isotopes with oxygen isotopes to expand the detectable scales of animal movements. Oxygen isotopes measure independent physical processes reflected in precipitation and are further modified by geospatially defined parameters, including continental positioning, orographic effects, amount of precipitation, humidity, and seasonality (Gat, 1996; Gat et al., 2001). To date, seasonality has received the most attention as a tractable source of oxygen isotope variation, which has enabled the characterization of animal birthing seasons from seasonal δ^{18} O values recorded in tooth enamel (Balasse et al., 2012b; Frémondeau et al., 2012; Henton et al., 2010; Tornero et al., n.d.; Towers et al., 2014). In studies seeking to isolate animal mobility using oxygen isotopes, analysts have encountered problems stemming from high seasonal fluctuations in ¹⁸O availability in study regions, which impedes the identification of areas on the landscape as having been accessed by livestock (e.g. Chase et al., 2014; Sjögren and Price, 2013; Valenzuela-Lamas et al., n.d., in press). Archaeologists have also explored using the range of δ^{18} O values within a sample of sequentially analyzed teeth as a measure of 58

distinct land-use strategies, including the practice of vertical transhumance (e.g. Henton et al., 2010; Mashkour et al., 2005). However, the difference between high and low δ^{18} O values is more suitable for the characterization of overall seasonal fluctuations in precipitation and temperature and cannot specifically differentiate movements across a landscape. Such approaches highlight the methodological challenges of characterizing local variation in the distribution of oxygen isotopes and tracking behavioral factors that modify the uptake of oxygen isotopes in seasonal environments.

In this chapter, we explore the ways in which oxygen isotopes obtained from incrementally sampled tooth enamel can be used to help identify vertical transhumance in domesticated bovids (sheep, goats, and cattle), livestock that are herded by pastoralists in regions around the world under a variety of environmental conditions. We draw attention to the importance of deciphering the shape of δ^{18} O curves obtained from incrementally sampled tooth bioapatite as a way to detect the movement of an animal between two locations positioned at different elevations, but receiving meteoric waters with distinct $\delta^{18}O$ signatures due to altitudinal fractionation effects. We explore the utility of using change points in the plots of a $\delta^{18}O$ time series by constructing an idealized model for a seasonal, continental environment – the Alps – that juxtaposes seasonality in precipitation δ^{18} O values against hypothetical animal mobility that takes place over short distances but over significant altitudinal gradients (ca. 2000 m). Finally, we highlight the limitations of our approach and outline future directions.

Pastoral livestock mobility: the strategy of vertical transhumance

The cultural anthropological literature abounds with economic, social, and behavioral definitions of pastoral societies (Barth, 1961; Browman, 1974; Cribb, 1991; Dyson-Hudson and Dyson-Hudson, 1980; Khazanov, 1994; Salzman, 2002; Spooner, 1971; Vainshtein, 1980; Vincze, 1980). While these definitions highlight variation in terms of political organization and ecological adaptation, they almost universally place mobility as a key characteristic that coordinates subsistence decisions and social interactions. Moreover, within any one pastoral system, mobility is not a uniform or static strategy, but an adaptive device that readily adjusts pastoral productivity through dynamic responses to natural and social environments.

Broadly speaking, vertical transhumance is a management strategy that entails the seasonal movement of domesticated livestock between lowland pastures, occupied in the winter, and high-elevation pastures,

grazed during the summer months. This seasonal round exploits the rhythms of pasture productivity available at different elevations and different times within a season. Vertical transhumance provides animals with access to higher forage biomass than would be available in any given location throughout the year, which improves yields of meat, milk, and wool for household consumption or exchange. Seasonal mobility for economic production also tends to increase social interactions with other migrating and sedentary groups, which provides opportunities for pastoral groups to negotiate complex social, political, and economic relationships (Barfield, 1993; Chang, 1993; Irons and Dyson-Hudson, 1972; Mansheev, 2009; Netting, 1981; Tapper, 1977).

The frequency and organization of vertical transhumance appears to be environmentally dependent but is also moderated by fluid social practices. In the mountainous regions of central and inner Asia, for example, continentality imparts extreme temperature and precipitation fluctuations between the summer and winter months. From mid-September to mid-May, snow and cold temperatures restrict access to upland pastures, and pastoralists settle in lowland areas, often as tribal conglomerations situated in so-called mobile villages (see also Evans-Pritchard, 1940; Frachetti, 2008; Khazanov, 1994; Shahrani, 2002). The timing of vertical movements of any one household or group generally follows the seasonal availability of pasture. One family may depart for higher elevations (1500-3000 m) in early May, but another might delay until mid-June, while others forgo vertical migrations altogether, as access to upland pasture is mediated through relationships of power, kinship, and patronage (Barth, 1961; Bauer, 2010; Ehlers and Kreutzmann, 2000; Vainshtein, 1980). Summer activities tend to emphasize the production of dairy products and general fattening of the animals, for which it is essential to provide high-density biomass and abundant water. Depending on the distribution of resources and territory, a seasonal round may consist of a few short (5–10 km) migrations to high-elevation pastures, followed by a descent at the end of the summer through regenerating pastures before finally settling in winter camps (Frachetti, 2008).

In the Alps, vertical transhumance is a well-known strategy practiced alongside intensive montane farming, known as "Almwirtschaft" (McGlynn, 2007). This practice of alpine agro-pastoralism is similar to the economic organization of Tibetan communities documented in the Himalayas (e.g. Bauer, 2010). Within this system, vertical mobility is limited to summer months, but unlike central Asian examples, residential mobility oscillates between permanent structures fixed onto a landscape partitioned between family estates organized by village councils (Cole and Wolf, 1974; Rhoades and Thompson, 1975). Alpine exploitation is focused heavily on growing grains (and potatoes) for human consumption in village fields. To sustain pastoral productivity, hay, harvested from cleared forest plots, is also produced in order to feed livestock during the winter. As nearly all arable land surrounding the villages is used for farming, animals are herded to high pastures to be fattened from late May to late September when they return as the hay harvest begins and begin fodder consumption (Fassio et al., 2014; Vincze, 1980; Zanini, 2013). As the short growing season of the summer months is used to provide an entire year's worth of sustenance and income from market sales, Almwirtschaft demands the orchestration of an extraordinary labor force recruited through flexible networks of kinship and land ownership (Cole and Wolf, 1974; Vincze, 1980). Almwirtschaft, while associated with a distinct social organization, represents another example of the importance of pastures at high elevations in feeding livestock to achieve sufficient levels of productivity.

Archaeological case study of vertical mobility

Establishing the ways in which high-elevation ecosystems were exploited in the past is crucial for understanding the multicentered emergence and spread of pastoral economies (Henn et al., 2008; Lees and Bates, 1974; Zeder, 2008). The developmental trajectory of pastoral societies in central Asia offers a cogent example. During the late Neolithic, agro-pastoral societies steadily advanced along the foothills and oases east and north from the Iranian Plateau into present-day Afghanistan and Uzbekistan (Harris, 2010). Early Bronze Age pastoralists are presumed to have developed economies focused on sheep and goat herding in the mountain ranges of central Asia while communities in the western and central steppe regions developed subsistence economies predominantly focused on the exploitation of cattle and horses, respectively (Bendrey, 2011; Frachetti, 2012). These regional trajectories later grew into interaction networks of mobile communities and connected distant regions, over which material culture, technology, and agricultural products were readily exchanged (Anthony, 2007; Frachetti, 2012; Linduff and Mei, 2009). As part of this complex of communities, Bronze Age mountain dwelling pastoralists have recently received increasing attention. The earliest direct evidence for the regional transmission of Southwest Asian and East Asian domesticated grains was discovered at high-elevation campsites in eastern Kazakhstan (Doumani et al., 2015; Spengler et al., 2014). This find raises critical questions about the flexibility of pastoral economies and behavioral factors leading to subsistence change. It remains to be seen, however, what role seasonal mobility played in providing access to domesticated grains and knowledge of cultivation, and whether pastoral strategies were modified as a result of increased investment in farming or perhaps stimulated the initial uptake of subsistence farming.

A direct measure of herding animals to high-mountain ecosystems would provide critical insight into the nature of Bronze Age Inner Asian food systems. Isotopic analyses of animal remains recovered from pastoral contexts can provide a direct and independent line of evidence that can help resolve the timing, magnitude, and frequency of vertical transhumance. Information about each of these qualities can inform a fine-grained picture of pastoral strategies and how they relate to socioecological processes, such as risk-minimizing behaviors (Mishra et al., 2003; Winterhalder et al., 1999), grazing intensity (Speed et al., 2012, 2013), territoriality (Dyson-Hudson and Smith, 1978), or the selection of traits to adapt livestock to specific environments (Klopčič et al., 2009; Saab et al., 2008; Shimada and Shimada, 1985). The implications of detecting vertical transhumance extend into the cultural realm as well, as quantitative information on mobility can feed into exchange network and social interaction models frequently invoked to explain how pastoral societies elicited technological innovations and material transfers to wider regions (Doumani et al., 2015; Tehrani et al., 2010) and promoted the formation of geographically vast cultural institutions and complex political spheres (e.g. Alizadeh, 2010; Frachetti, 2012; Porter, 2012). If oxygen isotopic data could add more detailed information about vertical strategies, then archaeologists would be better able to express these specific mobility behaviors as demonstrable actions that subsequently factor into reconstructions of social processes. An analytical approach on generating seasonal records of oxygen isotope values obtained from domesticated animal tooth bioapatite provides a way to build these critical datasets.

Environmental and biological variation of $\delta^{18}O$

The hydrological cycle and biological uptake

The distribution of oxygen isotopes is mainly driven by the global hydrological cycle, which fractionates oxygen isotopes through physical processes, including precipitation rainout, evaporation, and condensation (Gat, 1996; Gat et al., 2001). Bodies of water undergoing evaporation become enriched in ¹⁸O as water with lighter isotopes evaporates more readily; consequentially, precipitation is enriched in ¹⁸O while air masses become depleted as they travel overland (Cappa et al., 2003; Dansgaard, 1964). Temperature changes also add to the dynamic: as an air mass cools, it cannot hold as much water vapor, and heavier water molecules

precipitate out preferentially as part of Rayleigh distillation processes (Dansgaard, 1964). The relative amount of precipitation further influences meteoric water isotopic composition, as smaller rain droplets equilibrate with surrounding air masses, especially in hot and arid conditions, resulting in higher precipitation $\delta^{18}O$ values compared to rain forming in larger drops (Scholl et al., 2009; Yapp, 1982).

These fractionation effects are significant as air masses encounter mountains and are orographically lifted to higher altitudes. The precipitation caused by this uplift produces large amounts of rain as air masses rapidly condense; resulting precipitation is progressively depleted as ¹⁸O-enriched water is rained out. At higher elevations, secondary enrichment of rain droplets by evaporation during free fall is limited, as rain falls over a shorter distance, and mountain air is cooler compared to lower elevations (Araguás-Araguás et al., 2000; Scholl et al., 2009). The effects that mountains have on the transport of water vapor produce predictable patterns of δ^{18} O values in precipitation as a function of altitude and geographic positioning relative to prevailing winds, which have been observed in mountain ranges around the world (Bowen and Wilkinson, 2002; Dansgaard, 1964; Poage and Chamberlain, 2001; Siegenthaler and Oeschger, 1980). Because the isotopic composition of meteoric water is sensitive to such climatic and geographic factors, it can be used as a proxy for understanding the seasonality and provenance of certain biological tissues.

For the purposes of understanding the distributions of oxygen isotopes in bioapatite as a measure of vertical transhumance, it is important to consider drinking behavior of herbivores and water sources of δ^{18} O variation, including surface water and leaf water. The oxygen isotopic composition of plant tissues are, at any given time, a function of the isotopic composition of water that is absorbed by a plant root system; the oxygen isotopic composition of leaves in particular is affected by evapotranspiration through open stomata (Barbour, 2007; Ogée et al., 2007). Evaporation at the stomata-atmosphere interface results in an often significant enrichment in leaf water ¹⁸O, especially in hot and dry environments (Flanagan et al., 1991; Helliker and Ehleringer, 2000). As herbivores obtain much, if not all, of their water requirements from leaf water, the oxygen isotopic composition of their body water can be enriched in ¹⁸O relative to local precipitation (Kohn, 1996; Kohn et al., 1996; Longinelli, 1984; Wolf et al., 2011). As nonobligate drinkers, goats tend to drink less water than sheep due to water conservation adaptations, which allow goats to browse on more fibrous leaves and stems, containing more water than the less-fibrous grasses on which sheep preferentially graze (Al-Ramamneh et al., 2010; Silanikove, 2000a). Consequentially, goats can show a larger leaf-water oxygen

isotope signal than sheep and other obligate drinkers (e.g. Wang et al., 2008). Obligate drinkers require water on a regular basis from surface sources.

Often, surface waters reflect local meteoric δ^{18} O values, but this relationship depends on properties of the body of water that affect evaporation and subsequent enrichment in ¹⁸O relative to input water. Evaporative enrichment in lakes and ponds is a function of the ratio between volume and surface area, in addition to inflow and outflow rates, ambient temperature, and humidity (Leng and Marshall, 2004). Herders also construct artificial basins and troughs to store water for livestock to drink, which also become enriched in ^{18}O as these standing waters evaporate. The $\delta^{18}\text{O}$ values of such sources can significantly contribute to the body-water composition of an animal. In hot, dry, windy climates, at higher elevations, or during physical activity, herbivores lose more water by exhalation and transdermal evaporation of water (Levin et al., 2006; Schoeller et al., 1986; Silanikove, 2000b), which temporarily enriches body water ¹⁸O and demands water replenishment from open sources. Animals that are frequently moving or intensively milked will require dramatically more drinking water (Murphy et al., 1983), causing body water to reflect δ^{18} O values of drinking sources.

Throughout the year, an animal will be exposed to water sources with varying oxygen isotopic compositions. These include meteoric waters, which gradually and predictably shift over the course of the year, or ponds that undergo evaporative enrichment in ¹⁸O. Depending on the dynamics of the wider watershed of any given area, surface water sources will have δ^{18} O values that can be out of sync with the oxygen isotopic composition of local precipitation. The oxygen isotopic composition of river water generally reflects the δ^{18} O values of recharge sources. In several regions of the world, river water reflects δ^{18} O values of winter precipitation derived from snowmelt that infiltrates into the groundwater system where it is discharged without much change in ¹⁸O abundance, whereas river water undergoes evaporative enrichment in ¹⁸O as it flows over greater distance (Gat and Gonfiantini, 1981). Varying inputs of ¹⁸O are further modulated by an animal's own reservoir effect, since the rate of body-water turnover occurs between 7 and 21 days as a function of local weather conditions, the physical demands of pastoral production, and individual and taxon-specific variation (Abeni et al., 2015). The temporal variability of oxygen isotopes in body water is a relatively short-term rolling average of fractionation effects of water inputs and body-water loss, which present challenges for the purposes of tracking how environmental water sources and productive strategies of pastoral economies contribute to $\delta^{18}O$ values recorded in tooth enamel.

$\delta^{18}O$ time series of animal teeth

Tooth enamel is a highly mineralized tissue used in a wide range of archaeological stable isotope analyses, as is it durable against diagenetic alteration (Hillson, 2005). The primary mineral in tooth enamel is hydroxyapatite, represented by the chemical formula $Ca_{10}(PO_4)_6(OH)_2$, in which carbonate (-CO₃) can substitute for the phosphate (PO₄) and/or the hydroxyl (-OH) moieties (Elliott et al., 1985; Shi et al., 2005). Enzymatic reactions of ATPases and carbonic anhydrase rapidly interchange oxygen molecules between phosphate or carbonate and water (Faller and Elgavish, 1984; Hibberd et al., 1985; Uchikawa and Zeebe, 2012; Watkins et al., 2013), pegging δ^{18} O values of hydroxyapatite to those of body water (Blake et al., 2005; Hackney et al., 1979; Lécuyer et al., 2010). In this chapter, we will focus on the carbonate fraction, rather than the phosphate fraction, as oxygen from carbonates can be simultaneously analyzed alongside carbon isotopes and is easier to disassociate than it is to do so from phosphates (Lee-Thorp, 2002).

The enamel layer of hypsodont teeth is progressively formed during amelogenesis from the cusp to the cement-enamel junction. Once formed, enamel is biologically inert (Hillson, 2005; Smith, 1998). Amelogenesis is divided into two main stages: first, microscopic layers of high-protein enamel matrix are laid down by ameleoblasts diagonal to the tooth surface, followed by a maturation phase whereby heteromorphous mineralization fronts advance along the tooth growth axis and replace the matrix with hydroxyapatite crystals (Fisher and Fox, 1998; Passey and Cerling, 2002; Robinson et al., 1978). As enamel crystals expand, the microscopic appositional layers mature into hardened enamel (Kierdorf et al., 2013; Simmer et al., 2010; Smith, 1998; Suga, 1982). Isotopic inputs of an animal are incorporated into enamel over the extended maturation phase, which results in time averaging on the order of several months (Balasse et al., 2012b; Zazzo et al., 2005).

Time series isotopic data are obtained from animal teeth by drilling 1-2 mm bands of enamel perpendicular to the long axis on the buccal side of a mandibular tooth loph (e.g. Balasse et al., 2003). This method invariably crosscuts numerous appositional layers formed at different times and introduces additional time-averaging effects for the isotopic values of each sample band (Zazzo et al., 2005). Shifting the angle of the sampling bands does not alleviate the degree of time averaging (Balasse, 2003). Furthermore, sampling from the thinner layers of enamel located on the mesial side of bovid teeth showed only marginal improvement in temporal fidelity (Zazzo et al., 2012). The complexity in the directionality and duration of tooth enamel formation means that subsampling in bands along the tooth loph introduces an unknown amount of time averaging in obtained isotopic values. One method that seems to overcome some of the time-averaging effects involves sampling from the innermost enamel layer adjacent to the enamel-dentine junction using secondary ion mass spectrometry, which only requires a few micrometers of enamel (Blumenthal et al., 2014). While this technique produces high-fidelity measurements of $\delta^{18}O$ values relative to oxygen isotopic input signals, complicated sample preparation and the need for a scanning electron microscope are required. Nevertheless, time-averaging issues remain complicated by the fact that tooth growth rates are not uniform and tend to exponentially slow down over the course of tooth formation (Bendrey et al., 2015; Montgomery et al., 2010; Zazzo et al., 2012).

For the moment, there is a general consensus that despite these difficulties, the most pragmatic approach is to continue enamel sampling by drilling bands along the outer enamel surface on the buccal side of mandibular teeth (Balasse et al., 2012b; Chase et al., 2014; Henton et al., 2010; Towers et al., 2014). In experimental settings, where livestock do not wander to higher elevations and water sources reflect the oxygen isotopic composition of meteoric water, time series of $\delta^{18}O$ values present as a sinusoidal curve with maxima and minima values corresponding to summer and winter seasons, respectfully (Balasse et al., 2012b, 2002; Kohn et al., 1996). However, δ¹⁸O curves obtained from archaeological specimens often contain aberrations in this S-shaped curve, which need to be closely examined as they can provide information about mobility strategies providing livestock access to areas with distinct distributions of ¹⁸O variation.

VERTICAL TRANSHUMANCE AND OXYGEN ISOTOPES

Vertical transhumance exposes domesticated animals to pronounced variation in geospatially sensitive oxygen isotopic variability, and consequentially, it should be possible to detect such elevation changes in time series of $\delta^{18}O$ values recorded in tooth enamel. Much work has been done on developing reliable oxygen isotopic methods to detect aspects of animal management, in particular relating to studying birthing season (Balasse et al., 2012a; Henton et al., 2010; Stevens et al., 2011; Towers et al., 2014, 2011). However, archaeologists have only begun to delve into utilizing oxygen isotopes in a time series to infer the movement of domesticated animals (Chase et al., 2014; Sjögren and Price, 2013; Valenzuela-Lamas et al., n.d.). Some studies have relied upon oxygen isotopes in bulk collagen and enamel from animal tissues to evaluate animal mobility more generally (Cormie et al., 1994; Hoppe, 2006; Makarewicz and Tuross, 2012), which provide some insights into

averaged movements that occurred over the lifetime of an animal (but see Kirsanow et al., 2008, for the potential of organic $\delta 180$ values derived from sequentially or incrementally sampled tooth dentine). However, very little attention has been paid to the utility of oxygen isotopes in detecting vertical transhumance.

One proposed method to detect vertical transhumance using oxygen isotopes focuses on the range of δ18O values expressed in sequentially sampled enamel of modern sheep and goat third molars (Mashkour, 2003; Mashkour et al., 2005). Here, a vertical transhumance signal is claimed to be detectable in animals exhibiting a larger range of $\delta^{18}O$ values than in animals that are known to have been sedentary (Mashkour, 2003). This method was expanded upon by comparing the ranges in δ^{18} O values of sampled surface water taken along an elevation gradient in the study area to δ^{18} O ranges of sequentially sampled animal teeth to argue that larger ranges result from ingestion of local waters in highlands and lowlands as a result vertical transhumance (Mashkour et al., 2005). While this study highlighted the importance of examining pastoral mobility through isotopic measurement of herd animals collected from contemporary herds with precise information about their movement, the case that intratooth range in δ^{18} O values can reliably predict vertical mobility is confounded by movements that increase access to sources of water with distinct δ^{18} O values. For example, larger or smaller ranges in intratooth oxygen isotopes could be expected for animals consuming (1) substantial amounts of ¹⁸O-enriched leaf water or (2) isotopically variable ground and surface water sources that deviate from seasonal meteoric water δ^{18} O values.

An alternative approach involving the detection of lower maximum δ^{18} O values of an individual time series within an assemblage of higher values operates on the assumption that animals herded to higher elevations will exhibit lower summer season δ^{18} O values relative to those animals that remained at lower elevations, where δ¹⁸O values of summer season precipitation are higher (Henton et al., 2010). Notably, this method contradicts the logic of the previous method, which proposed that vertical transhumance is associated with a larger δ^{18} O range (e.g. Mashkour et al., 2005). Henton (2012) proposes that a δ^{18} O time series that appears flattened relative to the typical sinusoidal shape expected for seasonal environments is due to lower summer maxima δ¹⁸O values in teeth imparted by vertical transhumance movements.

It is not unreasonable to assume that animals spending summer months at higher elevations consume water depleted in ¹⁸O compared to lowland herded animals due to altitude effects on the oxygen isotopic composition of meteoric waters. However, the consumption of other sources of water available in areas not accessed by moving into highlands might also cause a depleted

¹⁸O signal. Groundwater, either consumed directly from discharging springs or indirectly through pastures growing in areas with a shallow water table, has been proposed as a confounding water source with purported steady δ^{18} O values that might also have a dampening effect on δ^{18} O values in animal teeth (Henton, 2012). It is important to remember that seasonal shifts in groundwater $\delta^{18}O$ values may be attenuated compared to local meteoric waters (O'Driscoll et al., 2005; Reddy et al., 2006), and therefore may have unintended consequences for the oxygen isotope curve measured in teeth. It is also possible that leaf water might contribute to a larger portion of body water during periods of low precipitation. Due to hot and arid conditions in Anatolia in summer, animals may need to drink more water from open sources characterized by lower $\delta^{18}O$ values than leaf water. This contribution to body water could cause a δ^{18} O time series to appear flattened in the summer months due to a lower proportion of leaf water enriched in ¹⁸O relative to drinking from streams without the animal having been moved to higher elevations. Given the difficulty of teasing apart the isotopic inputs of different water sources, detecting vertical transhumance in a time series of δ^{18} O values taken from the teeth of livestock remains challenging.

$\begin{tabular}{ll} Modeling vertical transhumance \\ And $\delta^{18}O$ values \\ \end{tabular}$

As an animal moves between elevation localities characterized by isotopically distinct meteoric waters, vertical moves should be detectable as slope changes in the δ^{18} O curve, reflecting the ingestion of water sources characterized by different δ¹⁸O values undergoing different seasonal changes. Such transitions in a time series are known as "change points" and are used to identify perturbations in time series, typically as a proxy for a understanding dynamics in complex systems, such as long-term climate change (e.g. Mudelsee et al., 2014; Ruggieri et al., 2009). As a heuristic device, we focus on looking for slope changes in a time series of δ^{18} O values sampled from livestock teeth as possible indicators of vertical movements that would have occurred during tooth development. We conceptualize this approach in order to provide a demonstration of expected shifts in δ^{18} O values based on idealized precipitation systems across mountain regions and how changes in δ^{18} O time series can occur when movements between lowland and highland locations are modeled with actual data of monthly δ^{18} O values in precipitation.

Here, we base our model on a pastoral seasonal round that entails movement from a lowland settlement to nearby mountain pasture and back in May and September, respectively. Using monthly δ^{18} O values measured

in precipitation from the Alps, we then explore how change points might be expressed and are influenced by the scheduling of migrations between lowland and highland localities characterized by seasonal shifts in the composition of oxygen isotopes in meteoric water. We model an ascent to summer pasture and descent to a winter camp as single moves that occur over a short period of time (i.e. less than a week). Pastoralists, such as the Qashga'i in Iran or Kazakhs on the Eurasian steppe, make horizontal movements that take several months (e.g. Bartold, 1962; Beck, 1991). However, it is not uncommon for vertical movements taking place in mountains between winter and summer camps, and vice versa, to occur in as little as three days (Khazanov, 1994; Vainshtein, 1980). We presume that time averaging caused by enamel formation and sample drilling (as previously discussed) is negligible enough not to obfuscate time-dependent patterns in a $\delta^{18}O$ curve sampled from molars developing during vertical moves. We restrict our analysis to observing change points in a δ^{18} O seasonal cycle as indictors of moving between locations with different oxygen isotopic values in meteoric water and not the detection of movement times, although based on the work done to determine birthing season, this reconstruction is theoretically possible (e.g. Balasse et al., 2012b, 2003; Towers et al., 2014).

In mountain systems around the world, the $\delta^{18}O$ values of meteoric water shift between -0.16% and

-0.40% per 100 m increase in elevation, which are most pronounced in the summer months (Garzione et al., 2000; Poage and Chamberlain, 2001; Siegenthaler and Oeschger, 1980). We take a conservative estimate of 0.20% per 100 m and expect a 4% offset in oxygen isotopes of precipitation over 2000 m between lowland and highland locations during the height of summer. Compared to the highland site, the lowland site would exhibit a greater seasonal range in δ^{18} O values of meteoric water, which causes greater seasonal increases and decreases of $\delta^{18}O$ values. The narrower seasonal range of δ¹⁸O values of precipitation falling at high elevations is due to the negligible effect of evaporative ¹⁸O enrichment of snow, in contrast to rain droplets (Siegenthaler and Oeschger, 1980). Even though meteoric water is not directly ingested by animals, it is frequently the primary contributor to the oxygen isotopic composition of surface water and water taken up by plants. We assume that ingested water at a high-elevation site is generally depleted in ¹⁸O relative to a lower-altitude site.

For an animal moving seasonally between such hypothetical sites, and assuming minimal reservoir effects, we expect a time series of δ^{18} O values to display distinct change points corresponding to vertical moves to areas with distinct trajectories of seasonal δ^{18} O values of meteoric water (Figure 5.1, blue curve). In this modeled example, a vertical move is simulated in late March at a time in the lowland site when δ^{18} O values

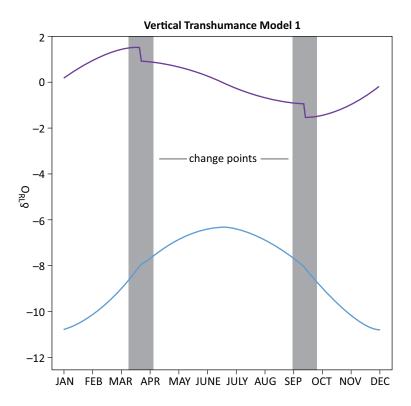


Figure 5.1. A theoretical model of continuous δ^{18} O values (blue) and the corresponding first derivative function (purple) throughout the year as recorded by a hypothetical molar from an animal that participated in a migration to highland pastures in mid-March until a mid-September return to the lowlands. Gray bars indicate timing of seasonal livestock herd movement.

of meteoric water are both higher in absolute value and seasonally increasing faster than the values of meteoric water at the highland site. Likewise, at the end of the summer season, when the animal is herded to lower elevations in September, the slope shift occurs in the opposite direction. This second change point develops in the time series as a result of moving into to the low-land environment with meteoric water $\delta^{18}O$ values that are simultaneously higher and decreasing more rapidly relative to higher-elevation sites.

One way to visualize these hypothetical transitions in the $\delta^{18}O$ curve is to think about the resulting vertical transhumant time series as containing changes in slope that can be characterized mathematically. The first derivative function measures the slope of the tangent at any given point in the $\delta^{18}O$ curve, which indicates the overall rate of change of the seasonal curve and highlights abrupt changes associated with vertical moves (Figure 5.1, red curve). In this hypothetical example, the first derivative function is characterized by a rapid

decrease in its values where a $\delta^{18}O$ time series suddenly shows a change in slope as an animal makes a vertical move. Essentially, rapid moves to different elevations are observed as "jumps" to a different seasonal progression of meteoric $\delta^{18}O$ values characteristic of each site.

Given that our model is focused on seasonal changes of the oxygen isotope composition of meteoric water, we now explore how actual data of δ^{18} O values of meteoric water from highland and lowland sites impart deviations to the idealized δ^{18} O time series of meteoric water between sites separated in elevation. We use monthly δ^{18} O data from two pairs of precipitation stations in the southern Alps and the Black Forest in southern Germany (Figure 5.2), as these regions provided the highest density of IAEA stations in an environment with substantial elevation differences. Each pair of stations is separated by a short horizontal distance (Weil am Rhein to Feldberg, 60 km, and Feletto to Villacher Alpe, 130 km), but by altitudinal differences representative of elevations meaningful to

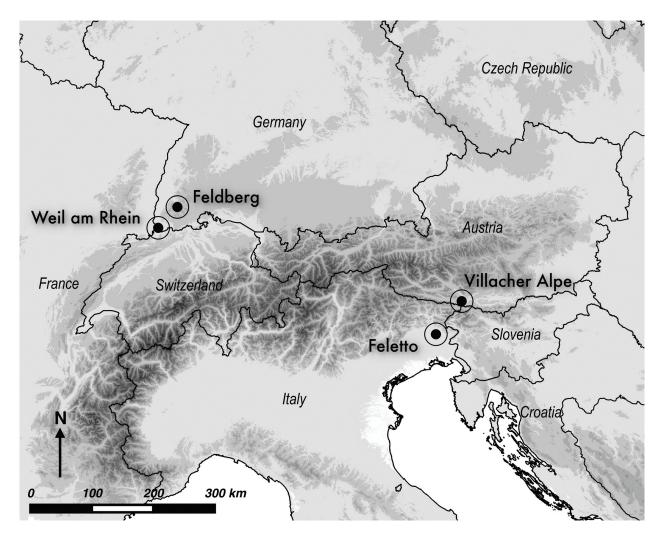


Figure 5.2. Map showing two pairs of lowland and highland sites used to model δ^{18} O values of meteoric waters available to livestock as part of a seasonal round of vertical transhumance: (1) Weil am Rhein in Switzerland (249 masl) and Feldberg in Germany (1493 masl); (2) Feletto in Italy (135 masl) and Villacher Alpe in Austria (2135 masl).

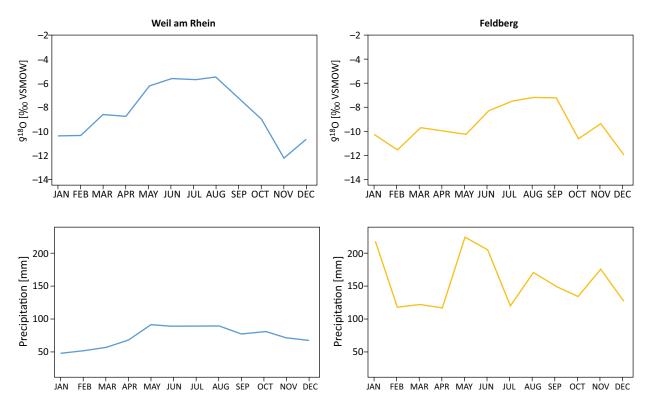


Figure 5.3. Average monthly δ^{18} O values and amounts of precipitation in Weil am Rhein (1988–2007) and Feldberg (1981–1987).

pastoralists practicing vertical transhumance (1244 m and 2000 m, respectively). Depending on data availability, monthly δ^{18} O and temperature measurements were averaged over several years (Weil am Rhein: 1988–2007, Feldberg: 1981–1987, Feletto: 1985–1987, Villacher Alpe: 1973–2002) in order to create a general pattern for these locations and reduce the impact of climatic anomalies (IAEA/WMO, 2015; Longinelli and Selmo, 2003). These data serve as a model of the seasonal meteoric water undercarriage of oxygen isotope availability at each location.

In Figure 5.3, Weil am Rhein and Feldberg in southern Germany show monthly average $\delta^{18}O$ curves that are broadly similar in shape, showing shallow sinusoidal curves with a small plateau in March, maxima across June and July, and minima in November, with an offset of ca. 2‰–4‰ between the two locations from May and August. Contrary to our assumptions presented previously in the idealized model, the autumn and winter values are more similar between the sites, which means a vertical move downslope may not cause a change point in the $\delta^{18}O$ curve.

To simulate a vertical move between Weil am Rhein and Feldberg, their respective $\delta^{18}O$ curves can be combined using segments representative of hypothetical time spent in each locality; that is, a modeled curve includes $\delta^{18}O$ values from the lowland site during the autumn, winter, and spring and $\delta^{18}O$ values from the highland site during the summer (Figure 5.4). This

approach does not act as a direct proxy for the integration of $\delta^{18}O$ values from meteoric water into tooth enamel but rather simulates exposure to different meteoric waters that characterize each location at particular times of the year.

The resulting curve, modeling δ^{18} O values expressed in an animal moving between the two sites in May and September, shows an abrupt decrease of $\delta^{18}O$ values (change point) at the time of the move to higher elevations in spring but remains fairly consistent during the autumn descent. A change is not observed during the descent because both locations share similar averaged δ^{18} O values of meteoric water at this time of year, as seen in Figure 5.3. The similarity of precipitation δ¹⁸O values between highland and lowland sites during the winter is characteristic of montane environments and is due to reduced evaporative altitude enrichment effect in snowfall; in contrast, there is wider disparity in summer season $\delta^{18}O$ values in meteoric water due to greater temperature difference between sites (e.g. Liebminger et al., 2006; Siegenthaler and Oeschger, 1980). The simulated ascent in May results in a depression of δ¹⁸O values that takes the form of a local maximum, followed by a skewed and suppressed curve leading to the global maximum that represents summertime spent at Feldberg. It is important to note that this sudden drop of δ^{18} O values associated with a simulated ascent is consistent with precipitation that is depleted in ¹⁸O as a result of sudden and intense downpours during a



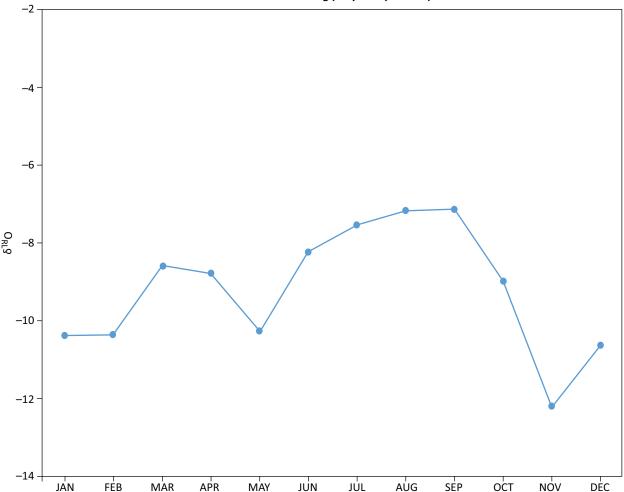


Figure 5.4. A modeled exposure to δ^{18} O values in precipitation based on a vertical move from Weil am Rhein to Feldberg in May and a return to Weil am Rhein in September.

short time period that impedes evaporative enrichment of rain during free fall, known as the "amount effect" (e.g. Higgins and MacFadden, 2004). To be sure, Figure 5.3 indicates that the most precipitation at Feldberg occurs during May with an amount close to 250 mm.

A different pattern is observed for simulated moves between Feletto Umbreto and Villacher Alpe stations, which are located in the southeast Alps and set apart by a distance of 130 km and elevation of 2000 m. Unlike Weil am Rhein and Feldberg, the average monthly $\delta^{18}O$ seasonal curves of Feletto Umbreto and Villacher Alpe are consistently offset by about 2‰–5‰ in summer, as well as during the winter, with the more southerly site of Feletto Umbretto exhibiting overall higher $\delta^{18}O$ vales of meteoric water (Figure 5.5).

By simulating a vertical transhumance seasonal round between Feletto Umbretto and Villacher Alpe with May and September moves, the modeled $\delta^{18}O$ curve exhibits the same change point as a decrease in $\delta^{18}O$ values during the spring move as the previous example (Figure 5.4), but in contrast, it also exhibits

a shift to higher values in the autumn, following a relatively flattened summer maximum appearing as a basin between the local maxima (Figure 5.6). A simulated seasonal round of vertical transhumance between locations characterized by relatively consistent offsets between monthly $\delta^{18}O$ values produces a $\delta^{18}O$ curve characterized by three local maxima.

The two pairs of locations demonstrate distinct patterns in the location of change points associated with vertical moves to and from higher elevation. It should be kept in mind that the $\delta^{18}O$ seasonal curves of precipitation as experienced by a vertically transhumant animal are dependent on the timing of movement, especially in cases where monthly $\delta^{18}O$ values track one another for part of the year and then exhibit a rapid offset, such as between Weil am Rhein and Feldberg (Figure 5.3). For simulated moves between Weil am Rhein and Feldberg, changes in movement timing prove to have dramatic impact on the shape of the simulated $\delta^{18}O$ curve. While a vertical ascent in April or May results in a local maximum followed by a small dip

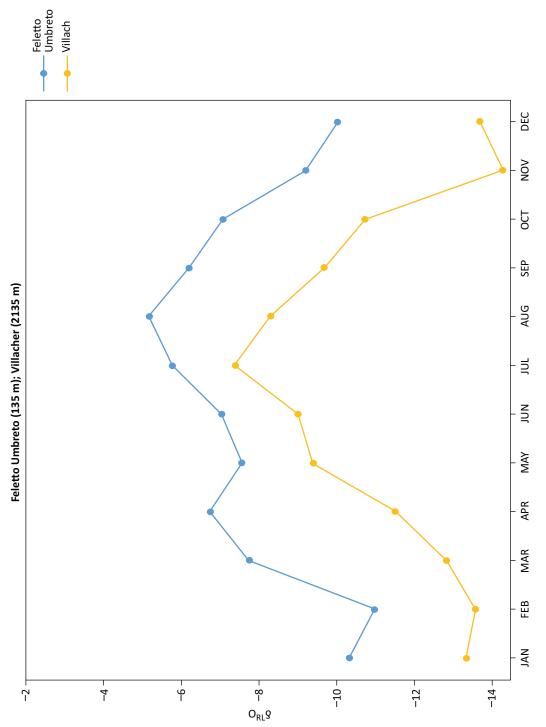


Figure 5.5. Average monthly 8180 values of precipitation in Feletto (1985–1987) and Villacher Alpe (1973–2002).

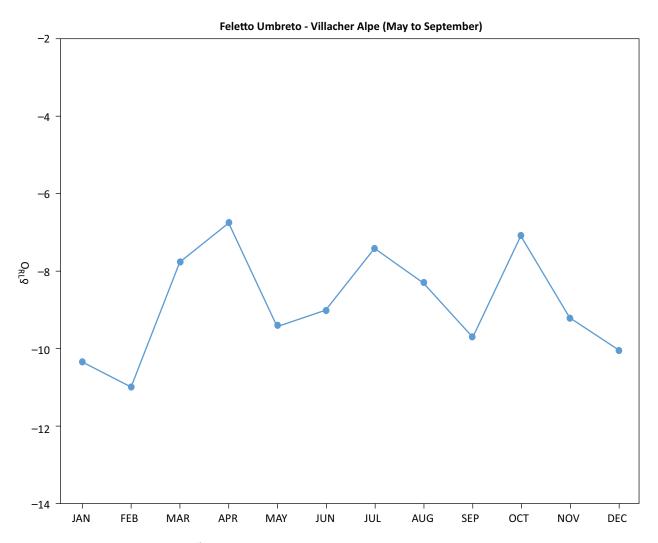


Figure 5.6. A simulated exposure to δ^{18} O values in precipitation based on a vertical move from Feletto to Villacher Alpe in May and a return to Feletto in September.

in the δ^{18} O curve (Figures 5.4 and 5.7), a move in June results in a simulated δ^{18} O curve displaying a more pronounced maximum that is significantly higher in value than a maximum value produced by earlier ascents (Figure 5.8). This prominent peak is a direct result of a move taking place between Weil am Rhein and Feldberg just after a period when the difference between average monthly δ^{18} O values of precipitation of Weil am Rhein and Feldberg was greatest (Figure 5.3). Essentially, an animal occupying Weil am Rhein would be ingesting simulated meteoric waters with δ^{18} O values of around -6‰ in May, but in June would suddenly be exposed to waters with δ^{18} O values of about -9‰ in Feldberg. This timing adjustment especially highlights the jump effect between two locations characterized by meteoric water with distinct oxygen isotope compositions.

Building off the idealized model presented at the beginning of this section, we demonstrate that using average monthly oxygen isotopic data of precipitation can dramatically affect the seasonal $\delta^{18}O$ inputs of ^{18}O available to livestock herded between highland and

lowland locations. The idealized model emphasizes the seasonal trends of $\delta^{18}O$ values in meteoric water that are caused by vertical moves and detectable as change points in the modeled time series. By using actual data from real locations, we show examples of temporal variation in the oxygen isotopic undercarriage as generated by differences in the scheduling in vertical transhumance strategies. Given these varied signals of vertical transhumance, the modeled $\delta^{18}O$ curves show two critical commonalities:

- 1. The presence of at least one but not more than two abrupt changes (change points) from one locally defined consistent slope to another
- The presence of peaks or valleys on the curve that are unusually pronounced given the overall trend of seasonal changes in ¹⁸O availability

Unless all livestock moves are timed to occur precisely within portions of the year when the $\delta^{18}O$ values of meteoric water for lowland and highland locations

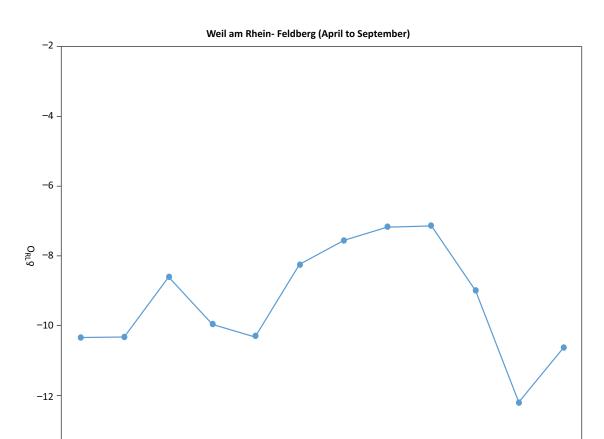


Figure 5.7. A simulated exposure to δ^{18} O values in precipitation based on a vertical move from Weil am Rhein to Feldberg in April and a return to Weil am Rhein in September.

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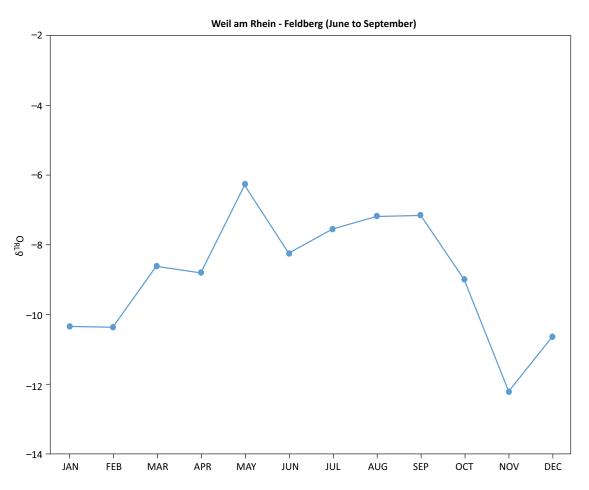


Figure 5.8. A simulated exposure to δ^{18} O values in precipitation based on a vertical move from Weil am Rhein to Feldberg in June and a return to Weil am Rhein in September.

overlap, sharp shifts in the curve will be visible. Our models suggest that analyses of $\delta^{18}O$ time series generated from sequentially sampled livestock molars should strive to move beyond the presentation of high and low values. A sole focus on the range of δ^{18} O values obtained from animal teeth will invariably conceal potentially revealing shapes of the δ^{18} O curves that may more directly indicate whether an animal had been moved to higher elevation pastures. We argue that analysts should focus on the portions of $\delta^{18}O$ curves that appear to indicate anomalies in the form of deviations from an idealized sinusoidal curve of $\delta^{18}O$ values across sample increments. As long as sampling errors are minimized when drilling teeth, these outlier data should be viewed as indices of valuable environmental and behavioral information when placed within an appropriate hydrological context.

DISCUSSION AND CONCLUSION

The seasonal availability of oxygen isotopes varies in locations separated by large elevations, and a domesticated animal exposed to these distinct oxygen isotope regimes through vertical transhumance should, we argue, reflect sudden changes in a time series sampled from a molar in development during such a seasonal round. As modeled previously, a vertical migration to summer pastures cannot be detected based on the range of δ^{18} O values present in a time series. When they are focused solely on low maxima of $\delta^{18}O$ time series relative to other maxima values in an assemblage, analysts could potentially be missing important isotopic signatures suggestive of vertical mobility. Furthermore, determining which maxima δ^{18} O values are considered low relative to other values in sets of δ^{18} O time series is an arbitrary process (e.g. Henton, 2012). It is possible to sample meteoric water or use modern monthly precipitation data to characterize the distribution of oxygen isotopes and then use these δ^{18} O values to predict the uptake of ¹⁸O by an animal in particular areas of interest. In such cases, knowing the monthly amounts of precipitation is important for understanding at what times of the year δ^{18} O values of meteoric water can be used as a reliable input source for δ^{18} O values measured in tooth bioapatite. In regions where precipitation is restricted to a few months out of the year, δ^{18} O values of tooth enamel formed during intense rain episodes will be more in sync with δ^{18} O values of local precipitation that are depleted in ¹⁸O compared to more regularly occurring and moderate precipitation cycles. This "amount effect" has been detected in $\delta^{18}O$ values taken from herbivore teeth in the deserts of the American Southwest (Higgins and MacFadden, 2004). During drier seasons, δ^{18} O values in animal tissues will be more

reflective of leaf water and local surface waters, which as previously discussed, are the products of various enrichment and transport processes.

Without δ^{18} O datasets characterizing various water sources in high spatial and temporal resolution, (cf. Henton et al., 2010; Mashkour et al., 2005), the utility of deciphering the hydrological context of a research area remains unrealized, despite obvious problems with using modern oxygen isotopic or precipitation data to represent past environments. For this reason, we propose examining δ^{18} O time series for effects that could indicate animal movement between distinct oxygen isotope regimes that focus on the expected oxygen isotope fractionation effects of vertical mobility, which are not necessarily reliant on independent modern measures of ¹⁸O or monthly amounts of precipitation in specific localities. We feel this standalone approach is more amenable to archaeological inquiry where paleoclimatic data in the form of paleoenvironmental proxies, let alone modern oxygen isotopic data, in research areas are often unavailable.

At the same time, it is important to recognize some limitations to our approach. Given that sequential sampling of animal teeth offers intra-annual resolution, it remains a possibility that snap changes to paleoenvironmental conditions are reflected in a regional hydrological cycle in such a way as to introduce similar critical points in a δ^{18} O time series. Furthermore, it is possible that rapid migrations covering great overland distances to northern latitudes might generate critical points in a time series, even if subtle. Given the differences in $\delta^{18}O$ values observed over elevation changes in the Alps, such a horizontal move would need to cover more than 1000 km in a short time as to generate a sudden change in slope in a δ^{18} O time series. Realistically, such a move would take 4-8 weeks to complete, as documented in 19th- and 20th-century Kazakh communities (Bartold, 1962), and would spread out the ¹⁸O gradient in such a way as to make the move undetectable in a time series. In this regard, detecting transhumance may only be possible if an animal made one-off moves between low- and highland areas separated by no less than ca. 1000–1500 m in elevation. As many pastoral strategies rely upon intermediate moves between winter and summer camps, such gradual encampments may not be detected.

Another drawback of our modeling is that the model does not factor in variation in $\delta^{18}O$ in local hydrology. We caution that the dynamics and accessibility of groundwater should be characterized for regions of interest, as these may introduce additional seasonal modifications of $\delta^{18}O$ values. During summer months the availability of surface water in mountains is mostly a product of melting snow and ice that accumulated in the winter season flowing into drainage basins; summer precipitation constitutes a smaller contribution to these

stream systems, as rain flows into these basins and also enters bedrock, from which its discharge can be delayed by several weeks (Foster and Allen, 2015; Mountain Research Initiative EDW Working Group, 2015). It is important to note that $\delta^{18}O$ values in meltwater from snow tend to increase 3%–5% during melting events (Taylor et al., 2002), which adds additional temporal variation in the oxygen isotopic composition of surface waters where snowpacks are present. As water flows to lower elevations and more readily evaporates from longer exposure to increasing temperatures, stream water becomes enriched in ¹⁸O (Koeniger et al., 2008), which causes waters initially depleted in ¹⁸O that accumulated at high elevation to reflect higher δ^{18} O values characteristic of lowland meteoric water. This distribution of ¹⁸O in surface water would parallel the variation observed solely by fractionation in precipitation. On the other hand, snowmelt often pools in basins that can be found at high altitude in fluvioglacial landforms, such as kettles and moraine plateaus, and can become significantly enriched in ¹⁸O as accumulated snowmelt evaporates (Leng and Marshall, 2004). Animals drinking these ¹⁸O-enriched sources of water at high elevation will take on uncharacteristic δ^{18} O values given their high-altitude dwelling (Figure 5.7).

Altitude effects similarly affect evapotranspiration in leaves and subsequent leaf water ¹⁸O enrichment rate, which increases with lower air pressure but also decreases with decreasing ambient temperature (Helliker and Ehleringer, 2000). Leaf water can further increase δ^{18} O values in animals, and for this reason, a thorough investigation of the botanical communities needs to be performed, which at least characterizes the proportions of grasses and dicots available in summer and winter pastures, as these taxa will exhibit different rates of ¹⁸O enrichment as a function of temperature and altitude (Barbour et al., 2001; Helliker and Ehleringer, 2000; Ogée et al., 2007; Terwilliger et al., 2002). In our model, we assume that leaf water enrichment in ¹⁸O is comparable between lowland and highland sites, or at least is not overwritten by local differences in meteoric water based on elevation. As leaf water fractionation effects are understudied, research exploring the range of oxygen isotopic values expressed in the leaf water of foliage ingested by livestock is greatly needed. Such data would be important for understanding the degree to which leaf water precisely impacts the oxygen isotopic composition of different taxa.

The model presented here is based on the oxygen isotope of meteoric water alone and does not consider the effects of delayed enamel maturation (e.g. Passey and Cerling, 2002) or nonconstant tooth growth (e.g. Bendrey et al., 2015; Montgomery et al., 2010; Zazzo et al., 2012), since these effects are unlikely to mask the development of change point in a δ^{18} O time series sequentially sampled from domesticated bovid teeth.

Controlled feeding experiments have shown that rapid changes to the dietary inputs of isotopes by manipulating δ¹³C values or through physiological changes in the rumen affecting δ^{13} C values fractionating by the gut microbiota can be readily detected in an isotopic time series sampled from enamel (Towers et al., 2014; Zazzo et al., 2005, 2010). While it should not be assumed that carbon and oxygen isotopes temporally track one another during tooth development, it is reasonable to assume that a detectable change in tooth enamel from manipulating the dietary input of carbon isotopes means that sudden changes in oxygen isotopes should be similarly conserved. These time-averaging issues are important for being able to detect via experimentation change points and curve shapes that indicate moves to environments with distinct availabilities of ¹⁸O. We stress that the shape of oxygen isotopic patterns derived from teeth, rather than the amplitude of isotopic change between summer and winter season oxygen isotope values, are crucial for the detection of vertical transhumance in livestock. However, we also emphasize that there are occasions where vertical movements by livestock are not reflected in the shapes of oxygen isotopic curves, and measurement of other isotopic species will be required. Additional research measuring the oxygen isotopes of sequentially sampled teeth of transhumant livestock with known life histories will help better tune the models presented here.

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Paper 3

Millet farming by early Bronze Age herders coincided with first crop transmissions across Eurasia

Taylor R. Hermes^{a,1} Michael D. Frachetti^{b,1} Paula N. Doumani Dupuy^{a,c} Alexei Mar'yashev^{d,2} Cheryl A. Makarewicz^{a,1}

¹To whom correspondence may be addressed. Email: trhermes@gshdl.uni-kiel.de, frachetti@wustl.edu, or c.makarewicz@ufg.uni-kiel.de.

²Deceased March 12, 2018

^aInstitute for Prehistoric and Protohistoric Archaeology, Graduate School "Human Development in Landscapes", Christian-Albrechts-Universität zu Kiel, 24118 Kiel, Germany

^bSAIE Laboratory, Department of Anthropology, Washington University in St. Louis, St. Louis, MO 63130, USA

^cSchool of Humanities and Social Sciences, Nazarbayev University, Astana 010000, Republic of Kazakhstan

^dInstitute of Archaeology, Almaty 050010, Republic of Kazakhstan

The authors declare no conflict of interest.

Author contributions: T.R.H. designed isotope research. M.D.F., A.M., P.N.D.D., and T.R.H conducted archaeological excavations. T.R.H. performed sampling and analyzed data. T.R.H., C.A.M., and M.D.F. interpreted the results. T.R.H. and C.A.M. wrote the paper with input from all authors.

Abstract

The dispersal of millet agriculture out of northern China in the early Bronze Age (third millennium BC) marked a pivotal development in transcontinental exchanges of domesticated plants and animals. After a long delay since domestication in the early Holocene, broomcorn millet was present in the steppe margins of eastern Kazakhstan by circa 2300 calibrated years (cal) BC, but a paucity of archaeobotanical evidence and also human remains for stable isotope analysis to measure dietary intake precludes resolving millet cultivation or its importance in human diets amid this initial crop transmission. However, livestock skeletal remains recovered from settlement sites of nomadic pastoralists are abundant. We report that by the first half of the third millennium cal BC pastoralists in the Inner Asian Mountain Corridor cultivated millet at scales large enough to provision their herds of sheep, goat, and cattle with agricultural by-product. Stable isotope analysis of livestock teeth reveals cycles of winter foddering with millet, and analysis of bone collagen demonstrates that foddering persisted over animal lifetimes. Intensive livestock foddering by pastoralists indicates that precocious cultivation coincided with the spread of millet into the steppe zone, implying that pastoralists had existing farming proficiency with Near Eastern domesticates.

Significance

Oxygen, carbon, and nitrogen isotope analyses of herbivore skeletal remains document the scale of millet agriculture amid its spread onto the Eurasian steppe. Mobile pastoralists in the mountains of Inner Asia since the first half of the third millennium BC were foddering domesticated bovids with cultivated millet, indicating that the initial transmission of millet agriculture westward out of China was accompanied by the knowledge and subsistence motivations to cultivate millet intensively. Subsequent shifts in the amount of millet foddering from the late Bronze Age into the Iron Age also shed new light on the evolution of synergistic farming and herding economies. These results provide a unique empirical basis to understand agricultural practice by nomadic pastoralists.

The transmission of domesticated plants and animals across Eurasia bridged distinct evolutionary trajectories of food production and helped humans reshape their agricultural niches to a wider variety of environments. Seasonal movements of mobile pastoralists in the Inner Asian Mountain Corridor (IAMC), linking montane ecotones from the Pamir to Altai Mountains, are thought to have facilitated cultural linkages and exchanges of domesticates between east and west Asia (1, 2). The arrival of Near Eastern cultigens of wheat (*Triticum* spp.) and barley (*Hordeum vulgare*), as well as cattle (*Bos taurus*), sheep (*Ovis aries*), and goats (*Capra hircus*), transformed the subsistence milieu of China by the second millennium BC (3–13). Broomcorn millet (*Panicum miliaceum*) became the first east Asian domesticated grain to spread west towards Europe sometime in the third millennium BC, followed by its cousin foxtail millet (*Setaria italica*) (14). Millets were domesticated in arid northern China in the early Holocene (15–17), and their hardy properties of rapid seeding time, drought tolerance, and no-till management were unique to agricultural systems using wheat or barley (18). By the end of the second millennium BC, millets were a staple food and risk-reducing crop throughout Eurasia (19–21).

The earliest known intersection of broomcorn millet, wheat, and barley took place in the foothills of southeastern Kazakhstan at Begash (22), a small pastoralist encampment supported by sheep, goat, and cattle herding, where carbonized seeds were found in a human cremation burial and directly dated to ca. 2460-2150 calibrated years (cal) BC (23). Nearby, at the early pastoralist site of Tasbas, a comparable but slightly older ceremonial context contained carbonized wheat seeds directly dated to 2580-2470 cal BC (24). The use of domesticated grains in mortuary settings in the mid-third millennium BC indicates that early pastoralists may have initially exploited food crops for ritual effect rather than subsistence needs, perhaps obtaining seeds through trade networks rather than from local harvests. By the mid-second millennium BC, people in the IAMC appear to have regularly consumed and cultivated millet, evidenced by high carbon isotope values (δ^{13} C) averaging ca. -15% (n = 11) in human bone collagen (25), coinciding with the earliest directly dated millet seeds in Europe (19). In the following millennium (1400-500 cal BC) agricultural production across the wider Eurasian steppe region intensified and expanded in breath to include broomcorn and foxtail millets as dietary staples, indicated by ubiquity of carbonized seed remains (26–29) and high δ^{13} C values in human bone collagen greater than –13‰ (30–37). While the macrobotanical record has provided insights into the timing of the initial transmission of millet across the steppe during the third millennium BC, the degree to which early Bronze Age mobile pastoralists invested in millet cultivation remains unclear.

Here, we investigate the use of millet as fodder for domesticated sheep, goat, and cattle through multi-stable isotope analysis of livestock skeletal remains in order to assess the intensity of millet agriculture from the early Bronze Age to Iron Age (ca. 2700 to 20 cal BC) in the IAMC—a crop transmission pathway of Eurasia (Fig. 1). The paucity of human remains so far recovered from archaeological sites dating to the early Bronze Age has impeded direct investigation of the carbon isotopic composition of human bone collagen, typically used to measure millet consumption across the steppe region (38). On account of intensive production of domesticated boyid meat, fat, milk, and fiber in pastoralist economies (39–41), rich assemblages of livestock skeletal remains provide a means to examine human manipulation of animal diets. In harsh steppe environments marked by strong seasonality and pasture shortages during winter, pastoralists frequently provision their animals with fodder in order to enhance herd security while meeting production goals for subsistence and social purposes (42–44). Fodder collected from natural pastures and stored for later use is a common strategy of steppe pastoralists (45), but cereal crop by-products (leaves, stalks, and chaff) can also be used after grains are harvested for human consumption, thus linking plant cultivation and animal husbandry into a more predictable and flexible subsistence base (46). We resolved high-resolution records of millet foddering by sequentially sampling livestock tooth enamel for carbon and oxygen isotopes in bioapatite ($\delta^{13}C_{apa}$ and $\delta^{18}O_{apa}$), which archive seasonal patterns of dietary intake (47–49) and cycles of ambient temperature via imbibed water (47–49), respectively. Carbon and nitrogen isotopic compositions of animal bone collagen (δ¹³C_{col} and δ¹⁵N_{col}) demonstrate lifetime dietary intake of millet biomass.

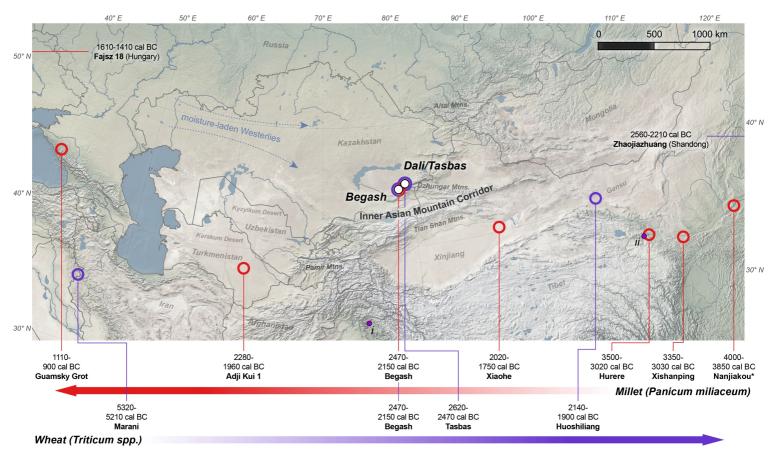


Fig. 1. Map of Asia illustrating sites sampled in the Inner Asian Mountain Corridor for stable isotope ratios of livestock remains (white circles). Direct radiocarbon dates on carbonized macrobotanical remains represent the chronology of millet spreading to western Asia from its homeland of domestication in northern China (red circles) and wheat into east Asia from the Near East (blue circles). Sites with directly dated barley remains are indicated by small violet circles: (i) Kanispur (2270-2240 cal BC) (12) and (ii) Gongshijia (2120-1890 cal BC) (5), which also include early third millennium BC dates in Pakistan and northern India that are beyond the map extent (12). See Table S1 for ¹⁴C data. Map projection is Lambert Conformal Conic with north along 70° E. Base imagery provided by Natural Earth.

Results and Discussion

C₃ Flora of the Inner Asian Mountain Corridor. Steppe biomes of Kazakhstan support C₃ vegetation that is dominated by bunch grasses (*Stipa* and *Festuca* spp.) and contain lower densities of sedges (*Carex* spp.), forbs (*Artemesia* spp.) and shrubs (*Spiraea* spp. and *Caragana* spp.), while in alpine areas, pine and juniper forests cover north-facing slopes and are intermixed with meadows (53). The Inner Asian Mountain Corridor (IAMC) receives high amounts of annual precipitation (400-800 mm) from March to November via moisture-laden Westerlies across Asia (Fig. 1) (50, 51), resulting in well-watered foothills and extensive groundwater stores accessed by steppe-desert plants (52, 53). Overall, the δ^{13} C values of C₃ steppe vegetation ranges from ca. –28 to –23‰ and is enriched in ¹³C by 2-4‰ during summer months due to water stress that reduces stomatal conductance to increase CO₂ recycling (54). Millets follow the C₄ photosynthetic pathway, which imparts high δ^{13} C values of ca. –12 ± 2‰ in plant tissues (54). Wild C₄ shrubs occur in low frequencies in hyper arid regions of the Kyzylkum and Karakum deserts where annual precipitation is less than 100 mm (52).

The carbon isotopic composition of contemporary and ancient herbivores confirms the predominance of 13 C-depleted C_3 plants in the IAMC and steppe-deserts of central Kazakhstan. Dietary δ^{13} C values for domesticated sheep, Central Asian red deer (*Cervus elaphus* ssp.), and saiga antelope (*Saiga tatarica*) fell between -27 and -22% (Fig. 2). Central Asian red deer graze throughout the year and regularly feed in lowland pastures that receive less precipitation than highlands (55). Dietary δ^{13} C values for steppe-desert dwelling saiga antelope, derived from summer

season hair growth (56), range from -25 to -22% and suggest minimal water stress in steppe-desert flora. Finally, low dietary δ^{13} C values of domesticated and wild herbivores from Kazakhstan and adjacent regions of Asia dating to the Bronze Age to the present suggest a long-term predominance of C₃ biomass throughout the Kazakh steppe zone (δ^{13} C means: cattle = -24.3%; caprine = -23.9%; saiga = -23.5%), in contrast to adjacent regions in Turkmenistan, China, and Mongolia, where dietary δ^{13} C values for herbivores can reach as high as -17% from consuming C₄ pasturage (SI Text 1).

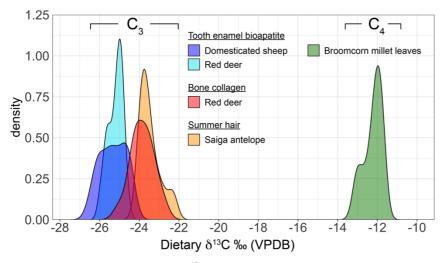


Fig. 2. Dietary mixing space between $\delta^{13}C$ values of broomcorn millet leaves sampled from modern plants (n = 17) in northern China (57) and dietary $\delta^{13}C$ values of wild and domesticated herbivores in Kazakhstan, reflecting consumption of C_3 -dominant vegetation. Three domesticated sheep and four ancient red deer gave intra-annual $\delta^{13}C$ values from tooth enamel bioapatite (n = 41 and n = 44, respectively), representing annual cycles of dietary intake in the IAMC and surrounding lowlands. Central Asian red deer (n = 19) sampled from early Bronze Age to Iron Age phases of IAMC archaeological sites, including one wild sheep (*Ovis ammon*) and one Siberian ibex (*Capra sibirica*) provided $\delta^{13}C$ values from bone collagen. Saiga dietary $\delta^{13}C$ values were derived from $\delta^{13}C$ values of summer hair from animals (n = 22) in a desert preserve in central Kazakhstan (56). Modern $\delta^{13}C$ values were corrected for the Suess effect (58). See Methods for trophic enrichment factors.

Ancient Livestock Foddered with Millet. The pastoralist sites of Begash, Tasbas, and Dali contain evidence for communities of herders subsisting on sheep, goat, and cattle since the third millennium BC (24, 40, 59), which are supported by a robust radiocarbon chronology of 58 AMS dates (Fig. S2-4). Styles and technologies of ceramics, metals, lithics, and architecture observed at the sites indicate that pastoralists in the IAMC were engaged in widespread and shifting cultural networks since the early Bronze Age (1, 60, 61). By performing cosine regressions on δ^{18} O_{apa} values, which largely record seasonal cycles of temperature reflected in meteoric water (62) and also rainfall amount to a lesser extent (63), we isolated intra-annual patterns in the consumption of C₄ biomass by sheep, goat, and cattle dating from the mid-third millennium to late first millennium BC (Fig. 3A-F). Ancient livestock from the IAMC exhibit a greater summer-time prevalence of $\delta^{13}C_{apa}$ values lower than -9\% that show animal diets exclusively derived from natural pastures, corresponding to dietary δ^{13} C values of less than -23%. High δ^{13} C_{apa} values in livestock intra-tooth sequences ranging from -11 to -3.2% largely coincide with low $\delta^{18}O_{apa}$ values associated with winter-season environmental inputs and are well above carbon isotope values for C₃ steppe biomes. Livestock ingesting C₄ plants outside their summer growth window suggests that people cultivated millet and, after harvest, stored by-products later used to provision their animals during the winter months. High $\delta^{13}C_{apa}$ values during cold months decrease with the onset of summer, a pattern that is consistent with pastoralists drawing from fodder stockpiles and then transitioning animal diets to steppe vegetation.

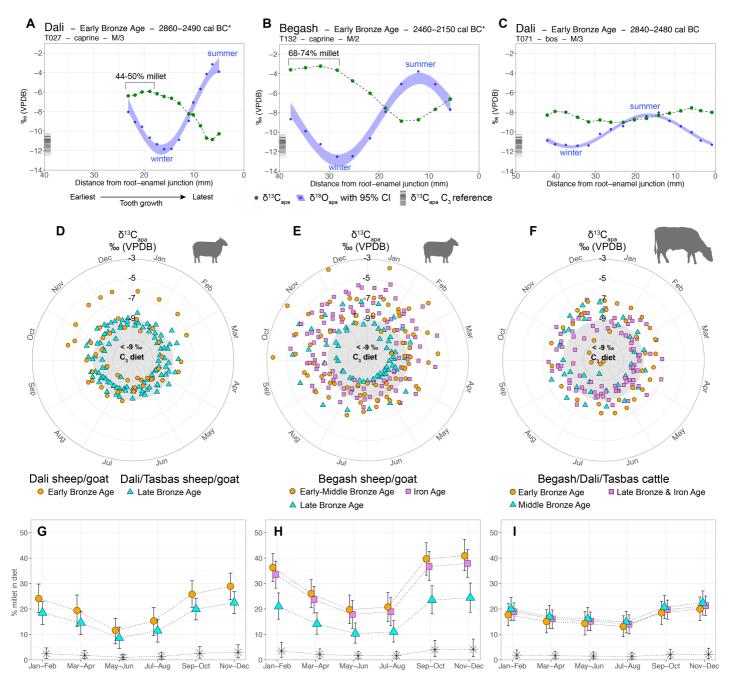


Fig. 3. Results of stable isotope analysis of livestock teeth and modelled dietary intake. (A-C) Time series of $\delta^{13}C_{apa}$ and $\delta^{18}O_{apa}$ values (including cosine fitting) in enamel bioapatite of second and third mandibular molars from livestock recovered from the earliest archaeological layers of Dali and Begash. (* Denotes directly dated individual; Table S2-3.) (D-F) $\delta^{13}C_{apa}$ values plotted as annual cycles. (G-H) Results of MixSIAR showing relative proportions of millet consumption plotted in two-month intervals with error bars representing 90% credible intervals. Black asterisks represent herbivores with a pure C_3 diet. Dali caprines: early Bronze Age (n = 4). Dali and Tasbas caprines: late and final Bronze Age (n = 6). Begash caprines: early-middle Bronze Age (n = 6); late Bronze Age (n = 5); Iron Age (n = 7). Dali cattle: early Bronze Age (n = 3). Begash cattle: middle Bronze Age (n = 3). Dali, Begash, Tasbas cattle: late and final Bronze Age (n = 8). List of teeth providing data is in Table S5, and site chronologies are in Tables S2-4. Raw data are in Dataset S1.

Intensive cultivation coincided with millet transmission. The earliest millet seeds in the IAMC at Begash were directly dated to the late third millennium BC (23), but how millet was used outside of burial contexts has remained speculative (64–67). We resolved the seasonal relative importance of millet in livestock diets by applying Bayesian mixing models (MixSIAR) to animal δ^{13} C values to estimate dietary proportions of food sources of steppe vegetation and millet by-products (Methods). Intensive foddering of livestock with millet at 2840-2480 cal BC is evidenced at Dali, representing the earliest known pastoralist communities in the IAMC. Out of four sampled sheep and goat teeth,

two exhibited high $\delta^{13}C_{apa}$ values of ca. -6% leading into cold months that correspond to ca. 44-50% dietary intake of millet (Fig. 3A,D), indicating stores of millet fodder were provisioned to caprines during the winter. Taken together, caprines from the early Bronze Age phase of Dali reflect about 30% dietary intake of millet (Fig. 3G).

Cattle $\delta^{13}C_{apa}$ values of ca. -7 to -8% through the winter correspond to about 10-20% dietary intake of millet, reflecting year-round consumption of agricultural by-product (Fig. 3F,I). It is important to note that cattle require up to six times more forage by weight than caprines (68), so that even a 10% dietary intake of millet represents a sizeable amount of fodder. Overall, $\delta^{13}C_{col}$ values greater than -18% from caprines and cattle substantiate lifetime dietary intake of millet by Dali livestock, including an individual cattle exhibiting a $\delta^{13}C_{col}$ value of -12.6% that reflects up to 60% millet intake (Fig. 4E). The foddering of livestock at Dali during the early-third millennium cal BC strongly suggests that the spread of millet was accompanied by the knowledge and skill sets required to intensively farm millet at levels that produced quantities of agricultural by-products sufficient to fodder herd animals during winter. This implies an earlier dispersal of millet agriculture west out of China than the macrobotanical record suggests, at least by 2840-2480 cal BC cal BC, which pushes back the chronology of farming in the IAMC by at least 1000 years (25, 66).

Millet agriculture appears to have intensified during the earliest occupation of Begash in the late third millennium BC (ca. 2400-1990 cal BC). Over two-thirds of caprines exhibited $\delta^{13}C_{col}$ values greater than -18%, including a prominent subset of values between ca. -13 and -12% that reflect ca. 50-60% millet intake during their lifetimes (Fig. 4A). Winter amounts of millet foddering increased during this period, as indicated by caprine teeth expressing winter $\delta^{13}C_{apa}$ values up to -3.2% (68-74% millet), followed by $\delta^{13}C_{apa}$ values less than -10% during summer (Fig. 3B). Seasonal surges of millet foddering were likely more pronounced than revealed in the isotopic tooth record of this early phase of Begash. As a point of reference, the caprine with the highest $\delta^{13}C_{apa}$ values in the assemblage exhibited a $\delta^{13}C_{col}$ value of -16% that modelled to about 20% millet over the animal's life (Fig. 4A), demonstrating that caprines with higher $\delta^{13}C_{col}$ values would likely reflect seasonal $\delta^{13}C_{apa}$ values in excess of -3%, perhaps having winter diets exclusively based on millet biomass. Similar intensities of millet foddering have been observed in Neolithic and Bronze Age village communities in China that heavily invested in millet as a dietary staple, where livestock commonly exhibit $\delta^{13}C_{apa}$ and $\delta^{13}C_{col}$ values greater than 0% and -8%, respectively, reflecting pure C_4 diets (15, 69, 70).

The scale needed to supplement livestock diets with millet biomass at levels observed in the IAMC demonstrates that early steppe pastoralists were well engaged in integrated farming and livestock husbandry, at least by the early third millennium BC. These synergistic investments likely enhanced herd security and strengthened production of animal goods, while simultaneously yielding grains for human consumption. We argue that the initial acquisition and adoption of millet by pastoralists in the IAMC were supported by pre-existing agricultural know-how, such that pastoralists, upon acquiring millet, were able to shape the cultivation of this novel crop to the harsh, seasonal environments of Central Asia and enhance their own subsistence niche. This process of cultural transmission is in sharp contrast to the delayed adoption of wheat and barley observed in Bronze Age China after these cultigens were introduced, reflecting social resistance to new crops prior to subsistence transformations (67). In the IAMC during the third millennium BC, intensive cultivation and ritual use of seeds at the fore of crop transmissions indicate that millet was readily assimilated into cultural logics without social barriers.

Shifts in Millet Cultivation in the Second and First Millennium BC. A conspicuous decline in seasonal millet foddering (Fig. 3D,H) from the middle to late second millennium BC corresponds to an overall trend of diminishing frequencies of livestock exhibiting high $\delta^{13}C_{col}$ values after the third millennium BC (Fig. 4A-D), suggesting a reduced importance of millet cultivation. A small number of livestock from the middle Bronze Age phase of Begash produced $\delta^{13}C_{col}$ values between -16 and -15%, while livestock from late Bronze Age layers did not exhibit $\delta^{13}C_{col}$ values above -16% (Fig.

4B). Late Bronze Age caprines exhibited reduced dietary intake of millet throughout the year and a minor seasonal rise compared to preceding and later cultural periods (Fig. 3H).

At Tasbas (1510-1200 cal BC), occupants locally farmed and processed barley and, to a lesser extent, wheat, broomcorn and foxtail millet, and green peas (26). Increased emphasis on barley, a hardy C_3 crop that grows well in environments with fewer growing-degree days that characterize high altitudes (7), like that of Tasbas (1500 m.a.s.l.), likely shifted fodder biomass to barley by-products, which is not readily detectable in δ^{13} C records due to similar carbon isotopic composition to steppe vegetation. However, about half of sampled caprines and cattle from all time periods of Begash received ¹⁵N-enriched diets (Fig. 4A-D), consistent with crops grown in manured fields (71–73). Livestock exhibit higher δ^{15} N_{col} values than that of wild herbivores (Mann-Whitney U = 2578; p < 0.0001; $n_{\text{livestock}} = 153$; $n_{\text{wild}} = 21$). A shift away from millet foddering is further evident by a loss of positive correlation between δ^{13} C_{col} and δ^{15} N_{col} values for the late Bronze Age, which is present for the early and middle Bronze Age phases of Begash (Pearson's r = 0.6589; p < 0.0001; n = 34 and Pearson's r = 0.4633; p = 0.0005; n = 53, respectively). Thus, livestock were likely still foddered intensively in the late Bronze Age but with more C_3 agricultural by-product.

During the Iron Age (310-20 cal BC), millet production returns to high levels, indicated by strikingly similar patterns in the intensity of caprine dietary intake of millet to that of the early-middle Bronze Age at Begash (Fig. 3H). Although millet foddering is less apparent in the carbon isotopic composition of livestock collagen in the Iron Age, due to a limited sample size from poor preservation in this phase (Fig. 4G), it is well documented that Iron Age mixed herding and multi-crop farming in the IAMC supported large villages with sophisticated irrigation networks (27, 39, 74). This has been argued to indicate social stratification, influential nomadic polities, and protracted interaction networks that characterized Iron Age society across the Eurasian steppe (75). That early Bronze Age livestock at Begash were foddered at levels similar to that of the site's Iron Age strongly suggests that third millennium BC millet cultivation strategies were equally reflective of expert food production.

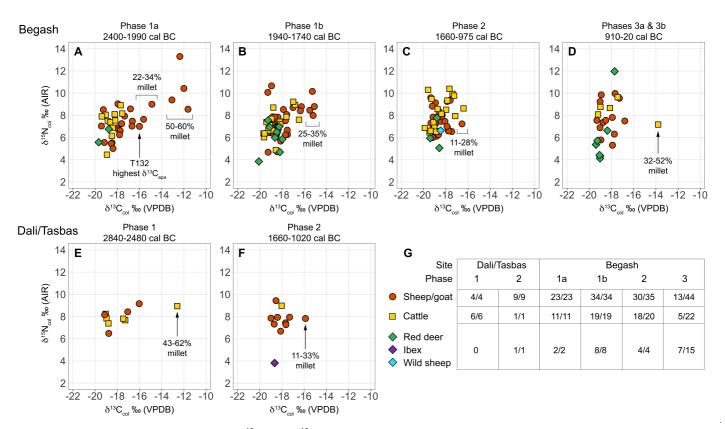


Fig. 4. Carbon and nitrogen isotope ratios ($\delta^{13}C_{col}$ and $\delta^{15}N_{col}$) of bone collagen from ancient livestock and wild ungulates in the IAMC. (A-D) Begash ca. 2400 to 20 cal BC. (E) Dali ca. 2840 to 2480 cal BC. (F) Dali and Tasbas ca. 1660 to 1020 cal BC. (G) Frequencies of accepted collagen samples based on C:N ratios between 2.9 and 3.6 (Methods). Poor preservation of collagen was observed in Begash phase 3. Raw data are in Dataset S2-3.

Conclusions

Starting in the early third millennium BC, pastoralists in the Inner Asian Mountain Corridor made significant investments in broomcorn millet cultivation, which allowed them to use stockpiles of millet fodder or fallow fields to supplement animal diets in the winter, thereby increasing pastoral production and reducing risk through diversified agricultural systems. This implies that the transmission of millet onto the Eurasian steppe coincided with the earliest intensive farming by steppe pastoralists. Large volumes of millet biomass consumed by caprines and cattle strongly suggest that their human handlers also likely adopted millet as food for themselves by harvesting grains and reserving leftover plant parts for animal fodder. Ruminants are inefficient at converting human-edible starchy grains into animal products, and doing so produces an overall energetic deficit (76). In addition to provisioning with harvested by-product, livestock were also likely used to clear stubble from fields after reaping, and dung was also likely used to enrich the next crop with nutrients (77). An emerging picture of pastoralist subsistence strategies from their first appearance during the early Bronze Age in the eastern steppe zone suggests that food economies were organized around deliberate connections between agricultural inputs and outputs, such that energy transfers between animals, crops, and people became more close-looped and conserved. This implies that third millennium BC pastoralists in the IAMC possessed the knowledge and skill sets to manage an energetically powerful food economy in the harsh environments of Inner Asia.

This study suggests an association between the timing of broomcorn millet dispersals west into the Eurasian steppe zone and the arrival of Near Eastern domesticated livestock to China, which were introduced not earlier than the third millennium BC (8, 13, 78–80). Although critical datasets remain sparse, it appears that the transmission of millet towards the steppe zone proceeded slowly across China via settled agriculturalists until communities of sheep, goat, and cattle herders encountered millet, perhaps as far as the eastern end of the IAMC in Gansu (Fig. 1), and readily recognized millet's versatility in enhancing livestock economies. As a new crop with unique properties compared to wheat and barley, pastoralists added millet to their toolkits of food production, which then spread at an accelerated pace through extensive social networks shaped by seasonal mobility patterns. That early pastoralists in the IAMC exhibited proficient use of millet to fodder livestock implies that prior combinations of animal management and farming of wheat and barley likely already existed in the IAMC, perhaps also across the wider steppe region. Our findings point toward deeper and more complex histories of pastoralist communities engaged in intensive plant cultivation and far-flung cultural transmissions.

Methods

Sampling Teeth. Bovid and cervid teeth were cleaned by sonication in distilled water, followed by abrasion with a scalpel to remove dental calculus and sediment accretions. Enamel powder was removed from a sequence of horizontal bands oriented perpendicular to the tooth growth axis on the buccal side of teeth from the top of the crown (earliest forming enamel) to its cervix (latest forming enamel) using a Dremel tool with a 1 mm wide tungsten carbide drill bit. Anterior tooth lophs were prioritized, and bands were spaced evenly, but sampling intervals and loph selection depended on tooth preservation. This sampling method has been demonstrated to capture time series of isotopic inputs via dietary intake that were integrated into tooth enamel bioapatite over the course of tooth development (81, 82). In general, second and third mandibular molars of sampled taxa form in the first and second years of life, respectively (83), which are not influenced by isotopic fractionation factors due to gestation, nursing, and rumen development (84). The temporal fidelity of tooth sequences represents integrated isotopic patterns that are attenuated due to the geometry of mineralization fronts, enamel maturation rates, tooth size and the inevitability of sampling across multiple appositional enamel layers (85). True magnitudes of isotopic shifts in tooth sequences are likely underestimated.

Enamel Pretreatment and Isotopic Analysis. Enamel pretreatment was performed at Archaeological Stable Isotope Laboratory, Kiel University, following Balasse et al. (86). Structural carbonates of bioapatite were analyzed for carbon and oxygen isotope ratios at the Leibniz Labor, Kiel University with a Finnigan MAT 253 mass spectrometer coupled to a Kiel IV device using reactions with 100% phosphoric acid. Analytical precision is 0.05% for carbon and 0.07% for oxygen. Measurements were calibrated using the carbonate standard NBS 19 ($\delta^{13}C = +1.95\%$ and $\delta^{18}O = -2.2\%$) and expressed relative to the international Vienna PeeDee Belemnite (VPDB) standard. All isotope ratios are reported in standard delta notation.

Bone Collagen. Skeletal remains from caprines, cattle, and wild herbivores were sampled from the faunal assemblage of Begash, Dali, and Tasbas. Collagen was extracted at the Archaeological Stable Isotope Laboratory, Kiel University, following Tuross et al. (87). Mass spectrometry for carbon and nitrogen isotope ratios was performed using a EuroVector Euro EA elemental analyzer coupled to a GVI IsoPrime in continuous flow mode at the Boston University Stable Isotope Laboratory. Analytical error was 0.1% for δ^{13} C and 0.2% for δ^{15} N. Isotopic values are expressed relative to VPDB for δ^{13} C and atmospheric nitrogen for δ^{15} N. Collagen samples with elemental C:N ratios between 2.9 and 3.6 were accepted for further analysis (88).

Modelling Dietary Intake. We estimated time of year using an approach adapted from Balasse et al. (62). Over annual rhythms of $\delta^{18}O_{apa}$ values, we modelled cosine periods to represent 365 "Julian days" with January 15th as day zero. Distance measurements were recorded for each sampling band from a fixed point at the root-enamel junction. This approach normalizes differences in tooth eruption and enamel maturation rates that vary between individuals (62). Statistical analyses were performed in R, version 3.4.1 (89).

Ontogenetic studies have shown that teeth exhibit an exponential decrease in growth rate (85, 90, 91). However, we did not observe declines in cosine fitting in tooth portions near the cervix, suggesting that isotopic attenuation due to enamel maturation mitigates slow-down effects. Controlled feeding experiments indicate a high-fidelity correspondence between dietary carbon and oxygen isotopic shifts and their integrations in animal tissues (85).

To model millet consumption as dietary percentages, we used the R package MixSIAR that generates Bayesian estimates of dietary intake (92–94). By calculating the means of $\delta^{13}C_{apa}$ sequences of each tooth by two-month intervals, we minimized error in calculating time of year. Community-level consumer data included mean $\delta^{13}C_{apa}$ values per archaeological time period at each site, and each two-month interval was parameterized as a fixed effect. Millet sources were represented by $\delta^{13}C$ values measured on leaves of broomcorn millet plants across China (n = 17) (57). C₃ steppe vegetation was represented by dietary $\delta^{13}C$ values derived from tooth enamel bioapatite of ancient red deer and modern sheep and also bone collagen of ancient red deer. Apatite $\delta^{13}C$ values were converted to dietary $\delta^{13}C$ values using a trophic enrichment factor (TEF) of 14‰ (95, 96). All carbon isotope values from modern plant and animal tissue were corrected for the Suess effect by adding 1.5‰ (58). In MixSIAR, C₃ sources were modelled using a TEF of 14‰ (95, 96), and for broomcorn millet a TEF of 12‰ was used for caprines (81). For cattle and red deer, 14‰ was used for both sources (95, 96). The TEF used for bone collagen on all ruminant taxa was 5‰ . Models were run with on three chains using uniform priors at 300,000 iterations with a burn-in of 200,000, followed by a 1:100 thinning.

Chronological Modelling. Begash and Dali are characterized by existing radiocarbon chronologies, and we obtained new radiocarbon dates for Dali, including those from faunal skeletal remains that were analyzed for stable isotopes (Table S2-3). Chronologies were modelled by phases with uniform priors using OxCal, version 4.3.2, and the INTCAL13 calibration curve (97).

Acknowledgments. We dedicate this work to Alexei Mar'yashev, who passed away shortly before submitting this paper. We thank colleagues who commented on this paper and ideas therein, including Miljana Radivojevic, Giedre Motuzaite-Matuzeviciute, Robert Spengler, and Britt Marie Hermes. We thank Nils Andersen of the Leibniz Laboratory of Kiel University for carbon and oxygen isotope analysis of bioapatite, in addition to Robert Michener of the Boston University Stable Isotope Laboratory for carbon and nitrogen isotope analysis of collagen. We greatly appreciate Tomasz Goslar of Poznan Radiocarbon Laboratory for running expedited ¹⁴C assays. This study was funded through the doctoral fellowship of T.R.H. at the Graduate School "Human Development in Landscapes" of Kiel University and through the Archaeological Stable Isotope Laboratory of Kiel University. The U.S. National Science Foundation funded archaeological excavations at Begash (Grants #0211431 and #0535341) and Tasbas (Grant #1132090). Excavations at Dali were funded by Washington University in St. Louis. Earlier versions of this paper were presented at the 7th International Symposium on Biomolecular Archaeology, Oxford, United Kingdom (2016) and the 82nd Annual Meeting of the Society for American Archaeology, Vancouver, Canada (2017).

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Supplementary Information

Millet farming by early Bronze Age herders coincided with first crop transmissions across Eurasia

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Table S1. ¹⁴C data displayed in Fig. 1 that shows chronology of crop translocations across Eurasia based on directly dated macrobotanical remains.

<u>Site</u>	Lab no.	Dated material	14C age (BP)	<u>Country</u>	<u>Culture</u>	<u>Reference</u>
Nanjiakou	N/A	N/A	N/A	China	Yangshao	(1); cited in (2)
Xishanping	TKa13889	b. millet	4490±35	China	Majiayao	(3)
Hurere	BA120182	b. millet	4530±60	China	Minhe	(4)
Xiaohe	BA05804	b. millet	3545±40	China	Xiaohe	(5)
Begash	Beta-266458	b. millet & wheat	3850±40	Kazakhstan	N/A	(6)
Adji Kui 1	LTL 15740A	b. millet	3708±45	Turkmenistan	N/A	(7)
Guamsky Grot	GrA-65,338	b. millet	2835±35	Russia	Kobyakovo	(8)
Fajsz 18	OxA-26704	b. millet	3214±36	Hungary	Sopot	(9)
Marani	Beta-368802	wheat	6290±30	Iraq	Halaf	(10)
Begash	Beta-266458	b. millet & wheat	3850±40	Kazakhstan	N/A	(6)
Tasbas	Beta-391200	wheat	4010±30	Kazakhstan	N/A	(11)
Huoshiliang	OZK603	wheat	3636±44	China	Siba	(12)
Zhaojiazhuang	BA061052	wheat	3905±50	China	Longshan	(13)
Kanispur	Beta-427232	barley	3880±30	India	N/A	(14)
Gongshijia	Beta-303689	barley	3620±30	China	Qijia	(4)

Supplementary Information Text 1. In order to evaluate the distribution of C₄ plants in Eurasia, we collected previously published δ^{13} C values from ancient and contemporary sheep/goat, cattle, saiga, and deer from northern China to western Turkmenistan (15–32) (Fig. S1). A sample of 584 δ^{13} C values indicates that C₄ intake is restricted to western Turkmenistan, China, and Mongolia, where herbivore δ^{13} C values are commonly greater than -18% and in many cases reach as high as -14% (Fig. S2). Notably, herbivore δ^{13} C values from the Eurasian steppe, which is largely represented by archaeological samples from Kazakhstan, strongly suggest an effective absence of wild C₄ biomass in the region. While the chronological range of the samples from the steppe region is not evenly represented across steppe micro-regions, including desert-steppe and forest-steppe biomes, it appears as though dietary intake of C₃ vegetation by steppe livestock remained predominant since the early Bronze Age. A small number of δ^{13} C values of caprine and cattle from northern and southern Kazakhstan and southwest Siberia were greater than -18‰ (Fig. S2-3), suggesting the possibility of dietary intake of C₄ plants, which could be millet fodder. The three highest δ^{13} C values were from the Iron Age, when millet agriculture was prevalent in the region, while two samples are from the early and late Bronze Age from sites at more northerly latitudes. These two latter cases may suggest a minor contribution of millet to animal diets or may reflect dietary intake of wild C₄ plants or ¹³C-enriched plants due to water stress. Modern samples providing δ^{13} C values from animal hair were converted to collagen values using methods described in the main text.

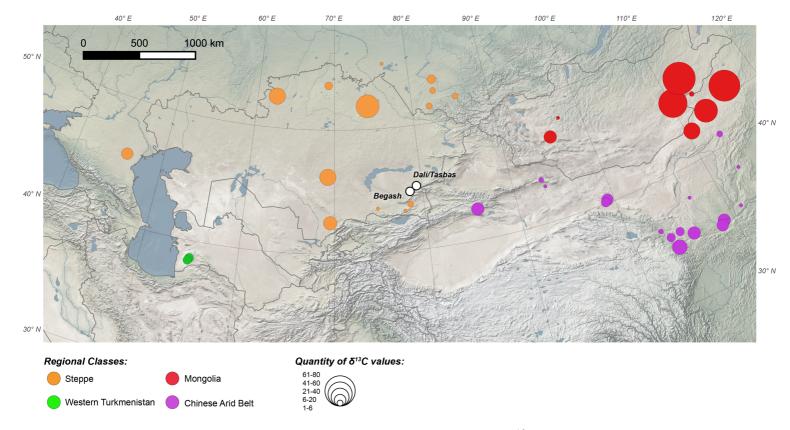


Fig. S1. Map of geographic distribution of previously published δ^{13} C values of domesticated and wild herbivores in the western steppe (15–19), Mongolia (17, 20, 21), western Turkmenistan (17, 22), northern and western China, referred to here as "Chinese Arid Belt" (23–32).

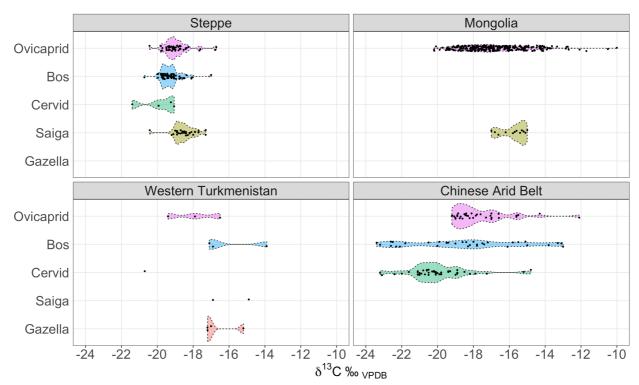


Fig. S2. Distributions of $\delta^{13}C$ values of domesticated and wild herbivores from four geographic areas of Eurasia.

			δ ¹³ C				
	Taxon	n	Mean	SD	Median	3 rd Quartile	
	Ovicaprid	44	-18.9	0.72	-19.1	-18.7	
	Bos	65	-19.3	0.55	-19.4	-19.1	
<u>Steppe</u>	Cervid	4	-19.9	1.06	-19.6	-19.2	
	Saiga	34	-18.5	0.59	-18.6	-18.2	
	Gazella	0	-	-	-	-	
	Ovicaprid	34	-17.6	1.57	-18.2	-17.0	
Chinese Arid	Bos	33	-18.5	3.08	-18.3	-16.1	
	Cervid	44	-20.0	1.65	-20.2	-19.2	
<u>Belt</u>	Saiga	0	-	-	-	-	
	Gazella	0	-	-	-	-	
	Ovicaprid	300	-16.8	1.77	-17.0	-15.7	
	Bos	0	-	-	-	-	
<u>Mongolia</u>	Cervid	0	-	-	-	-	
	Saiga	13	-15.8	0.68	-15.6	-15.2	
	Gazella	0	-	-	-	-	
	Ovicaprid	3	-17.9	1.45	-17.9	-17.2	
Western	Bos	3	-16.0	1.79	-16.9	-15.4	
	Cervid	1	-20.7	-	-	-	
<u>Turkmenistan</u>	Saiga	2	-15.9	-	-	-	
	Gazella	4	-16.7	0.97	-17.1	-16.6	

Fig. S3. Summary statistics of $\delta^{13}C$ values of domesticated and wild herbivores plotted in Fig. S2.

 Table S2. Radiocarbon chronology of Begash.

Phase	Lab no.	Material	Isotope sample no.	¹⁴ C age (BP)	2-sigma	Modelled Phase	Reference
1a	AA52926	charcoal	oumpio no	4220±220	3500-2200 cal BC	2400-1990 cal BC	(33)
1a	OS-54364	charcoal		3870±35	2470-2200 cal BC		(33)
1a	Beta-266458	b. millet & wheat		3840±40	2470-2150 cal BC		(6)
1a	Poz-88835	caprine bone	T132	3830±30	2460-2150 cal BC		This study
1a	OS-54365	charcoal		3800±35	2430-2060 cal BC		(33)
1a	Beta-266459	charcoal		3760±40	2300-2030 cal BC		(6)
1a	Beta-266460	charcoal		3740±40	2290-2020 cal BC		(6)
1a	Beta-266457	charcoal		3720±40	2280-1980 cal BC		(6)
1a	OS-54334	charcoal		3650±45	2150-1890 cal BC		(33)
1b	OS-54833	charcoal		3540±140	2290-1520 cal BC	1940-1740 cal BC	(33)
1b	OS-54328	charcoal		3500±30	1910-1740 cal BC		(33)
1b	OS-54333	charcoal		3490±30	1900-1690 cal BC		(33)
1b	OS-54329	charcoal		3460±35	1890-1690 cal BC		(33)
2	OS-54367	charcoal		3310±35	1690-1500 cal BC	1660-975 cal BC	(33)
2	OS-54000	charcoal		3100±50	1500-1220 cal BC		(33)
2	OS-54369	charcoal		2880±40	1210-930 cal BC		(33)
3a	AA52925	charcoal		2657±84	1020-540 cal BC	910-420 cal BC	(33)
3a	AA52927	charcoal		2435±47	760-400 cal BC		(33)
3a	OS-54366	charcoal		2430±45	760-400 cal BC		(33)
3b	AA52920	charcoal		2253±35	400-200 cal BC	310-20 cal BC	(33)
3b	AA52923	charcoal		2152±36	360-50 cal BC		(33)
3b	OS-54376	charcoal		2150±30	360-60 cal BC		(33)
3b	AA52924	charcoal		2142±41	360-50 cal BC		(33)
3b	AA52922	charcoal		2141±35	360-50 cal BC		(33)
3b	OS-54368	charcoal		2140±30	360-50 cal BC		(33)
3b	OS-54492	charcoal		2090±35	210-1 cal BC		(33)
3b	OS-54377	charcoal		2060±35	180 cal BC - cal AD 20		(33)
3b	OS-54818	charcoal		2050±80	360 cal BC - cal AD 130		(33)
4	AA52918	charcoal		1874±37	cal AD 60-240	cal AD 70-540	(33)
4	AA52917	charcoal		1853±40	cal AD 60-250		(33)
4	AA52916	charcoal		1852±53	cal AD 30-330		(33)
4	OS-54331	charcoal		1830±40	cal AD 70-330		(33)
4	OS-54363	charcoal		1700±35	cal AD 250-410		(33)
4	OS-54330	charcoal		1600±35	cal AD 390-550		(33)
5	AA52921	charcoal		715±33	cal AD 1220-1390	cal AD 1240-1420	(33)
5	OS-54378	charcoal		575±30	cal AD 1300-1420		(33)
6	OS-54160	charcoal		135±35	cal AD 1660-1950	cal AD 1670-1930	(33)
6	OS-54383	charcoal		110±25	cal AD 1680-1940		(33)
6	OS-54375	charcoal		100±30	cal AD 1680-1940		(33)

 Table \$3.
 Radiocarbon chronology of Dali.

Phase	Lab no.	Material	Isotope sample no.	¹⁴ C age (BP)	2-sigma	Modelled Phase	Reference
1	ISGS-A2837	charcoal	sample no.	4100±20	2860-2570 cal BC	2840-2480 cal BC	This study
1	Beta-484122	caprine tooth	T027	4080±30	2860-2490 cal BC		This study
1	Poz-92105	cervid bone		4040±35	2840-2470 cal BC		This study
2	ISGS-A2838	charcoal		3330±15	1670-1530 cal BC	1660-1460 cal BC	This study
2	Poz-92107	cattle bone		3300±30	1650-1500 cal BC		This study
2	Poz-92106	horse bone		3240±30	1620-1430 cal BC		This study
2	Poz-92109	caprine bone	:	3240±30	1620-1430 cal BC		This study
3	Poz-92110	caprine bone	T033	2950±30	1260-1050 cal BC	-	This study

Table S4. Radiocarbon chronology of Tasbas. (*Outlier excluded from modelled phase.)

Phase	ab no.	Material	Isotope sample no.	¹⁴ C age (BP)	2-sigma	Modelled Phase	Reference
1	OS-93050	charcoal	oumple no.	4100±30	2870-2500 cal BC	2850-2470 cal BC	(34)
1	OS-93054	charcoal		4060±30	2840-2480 cal BC		(34)
1	Beta-391200	wheat		4010±30	2620-2460 cal BC		(11)
2a	OS-93268*	charcoal		3670±45*	2220-1920 cal BC*	1510-1200 cal BC	(11)
2a	OS-93053	charcoal		3150±35	1510-1300 cal BC		(34)
2a	OS-92277	barley		3090±40	1440-1230 cal BC		(34)
2a	OS-91990	barley		3030±35	1410-1130 cal BC		(34)
2b	OS-97173	charcoal		2940±30	1260-1040 cal BC	1230-1020 cal BC	(11)
2b	OS-93052	charcoal		2930±30	1220-1020 cal BC		(11)
2b	OS-93051	charcoal		2920±25	1210-1020 cal BC		(11)
3	OS-97172	charcoal		2720±35	930-800 cal BC	-	(11)

Table S5. Herbivore teeth sampled for $\delta^{13}C$ and $\delta^{18}O$. Raw data are provided in Dataset S1.

Tooth ID	Site	Period	Phase	Taxon	Element	Symmetry	# samples	Direct date
T132	Begash	Early Bronze Age	1a	Caprine	M/2	right	11	Poz-88835
T131	Begash	Early Bronze Age	1a	Caprine	M/3	right	8	Poz-88835
T031	Begash	Early Bronze Age	1a	Caprine	M/3	left	19	1 02 00000
T001	Begash	Middle Bronze Age	1b	Caprine	M/3	ioit	10	
T003	Begash	Middle Bronze Age	1b	Caprine	M/3	left	18	
T003	Begash	Middle Bronze Age	1b	Caprine	M/3	left	6	
T032	Begash	Late Bronze Age	2	Caprine	M/2	left	13	
T112	Begash	Late Bronze Age	2	Caprine	M/3	right	16	
T113	Begash	Late Bronze Age	2	Caprine	M/2	left	10	
T113	Begash	Late Bronze Age	2	Caprine	M/2	right	14	
T115	Begash	Late Bronze Age	2	Caprine	M/2	left	8	
T014	Begash	Iron Age	2 3b	•	M/3	leit	14	
T014		Iron Age	3b	Caprine	M/3	right	18	
T018	Begash	•	3b	Caprine	M/3	left	14	
	Begash	Iron Age		Caprine	M/3			
T019	Begash	Iron Age	3b	Caprine		right	15 15	
T030	Begash	Iron Age	3b	Caprine	M/3	right		
T146	Begash	Iron Age	3b	Caprine	M/3	right	15	
T147	Begash	Iron Age	3b	Caprine	M/2	left	17	
T022	Dali	Early Bronze Age	1	Caprine	M/3	left	20	D-4- 404400
T027	Dali	Early Bronze Age	1	Caprine	M/3	left	14	Beta-484122
T050	Dali	Early Bronze Age	1	Caprine	M/3		5	
T085	Dali	Early Bronze Age	1	Caprine	M2	right	8	
T026	Dali	Late Bronze Age	2	Caprine	M/3	left	9	
T023	Dali	Late Bronze Age	2	Caprine	M/3	right	18	
T029	Dali	Late Bronze Age	2	Caprine	M/3	right	20	
T033	Dali	Final Bronze Age	3	Caprine	M/2	right	24	Poz-92110
T025	Tasbas	Late Bronze Age	2b	Caprine	M/3	right	5	
T024	Tasbas	Late Bronze Age	2a	Caprine	M/3	right	24	
T102	Begash	Middle Bronze Age	1b	Bos	M/2	right	14	
T103	Begash	Middle Bronze Age	1b	Bos	M/2	right	12	
T105	Begash	Middle Bronze Age	1b	Bos	M/1	right	10	
T110	Begash	Late Bronze Age	2	Bos	M/2	right	9	
T111	Begash	Late Bronze Age	2	Bos	M/3	right	10	
T117	Begash	Late Bronze Age	2	Bos	M/3	right	10	
T138	Begash	Late Bronze Age	2	Bos	M/2	left	10	
T013	Begash	Iron Age	3b	Bos	M/2		8	
T140	Begash	Iron Age	3b	Bos	M/2	right	10	
T071	Dali	Early Bronze	1	Bos	M/3	left	16	
T072	Dali	Early Bronze	1	Bos	M/3	right	16	
T096	Dali	Early Bronze	1	Bos	M/2	right	6	
T073	Dali	Middle Bronze Age	2	Bos	M/2	right	15	
T077	Dali	Middle Bronze Age	2	Bos	M/2		10	
T101	Tasbas	Final Bronze Age	3	Bos	M/2	left	11	
T127	Begash	Iron Age	3b	Cervus	M/3	right	17	
T129	Begash	Historic	6	Cervus	M/2	right	14	
T130	Begash	Historic	6	Cervus	M/3	right	7	
T157	Begash	Historic	6	Caprine	M/3	right	13	
T020	Bayan-Zherek	Modern		Caprine	M/2	left	21	
T021	Bayan-Zherek	Modern		Caprine	M/3	left	17	

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Mitochondrial diversity of ancient goats in Eurasia and translocation vectors of pastoralist economies into Central Asia

Taylor Hermes
Cheryl Makarewicz
Michael Frachetti
Dmitriy Voyakin
Paula Doumani
Antonina Erlomaeva
Giedre Motuzaite-Matuzeviciute
Alexei Mar'yashev
Almut Nebel

Abstract

Goats (*Capra hircus*) were domesticated in the Near East about 11,000 years ago and spread across Eurasia as an economically productive and environmentally resilient herd animal. While the geographic origins of domesticated goat lineages are well established, the pathways taken by pastoralists and agriculturalists that translocated goats across Asia during the early Bronze Age (ca. 3000 to 2000 cal BC) and later periods remain unclear. In this paper, we analyze the sequences of hypervariable region I and cytochrome *b* in the mitochondrial genome of Bronze and Iron Age goats from archaeological sites located along proposed translocation vectors into Central Asia. Since the late Bronze Age (ca. 1600-1000 cal BC), high genetic diversity was present in the Tian Shan and Dzhungar ranges of the Inner Asian Mountain Corridor, indicated by mtDNA haplotypes representing lineages A and C, in addition to the very rare D lineage. In contrast, only mtDNA haplotypes of lineage A were observed in the northerly "Eurasian steppe belt." These findings suggest that early herding communities living in montane ecosystems were drawing from genetically diverse goat populations, likely via the Iranian Plateau, while northern steppe communities had goats consistent with a founder population, possibly via eastern Europe.

Introduction

Domesticated goats (*Capra hircus*) are core animals for nomadic pastoralists and smallholding farmers around the world, providing dependable sources of meat, milk, hides, and fiber, while being able to thrive in harsh environments^{1,2}. Zooarchaeological data demonstrate that bezoars (*Capra aegagrus*), the wild progenitor of domesticated goats, were being preferentially culled as juveniles by about 11,000 years ago in eastern Anatolia and the Zagros Mountains^{3–5}, indicating that initial animal management followed a prey-pathway model of domestication⁶. By the eighth millennium BC, goats began displaying body size diminution and changes to horn morphology, which strongly suggests that domestication had effectively resulted in genetic isolation from sympatric bezoars^{7,8}. Six divergent mtDNA haplogroups (A, B, C, D, F, and G) in both domesticated goats and bezoars suggest that the process of domestication involved the recruitment of multiple maternal lines and/or introgression events that are likely to have occurred in more than one geographic region of the "Fertile Crescent" 11

Unlike cattle (*Bos taurus*) and sheep (*Ovis aries*), domesticated goats display contemporary mtDNA variation with weak phylogeographic structure, which has been interpreted to be the result of extensive translocation and population expansions of goats¹². However, this genetic patterning is probably more a product of recent demographic processes since the historical era than a reflection of early-mid Holocene human activity. For example, present-day frequencies of goat mtDNA haplogroups are heavily biased towards lineage A, which currently characterizes over 91% of analyzed specimens world-wide^{9–11}. As Neolithic communities radiated outward from the Fertile Crescent locus of plant and animal domestication, goats belonging to particular maternal haplogroups may have been transported to regions of Eurasia in distinctive frequencies. Reconstruction of ancient haplogroup frequencies and genetic phylogenies may be used to isolate geographic sources and termini of important vectors of human population movements and successive livestock gene flows.

Central Asia is a critical region for understanding the spread of domesticated plants and animals across the expanse of Eurasia and into east Asia, which likely occurred as a result of mobile pastoralists generally advancing eastward from the Near East^{13–15}. Presently, there are two dominant hypotheses concerning the routes for the spread of herding economies into Central Asia. The "Eurasian steppe belt," a relatively narrow ecotone of grasslands extending from eastern Europe to the Altai Mountains of southern Siberia, has dominated the archaeological discourse of cultural migrations within Central Asia¹⁶. Acting as an ecological channel for the movement of pastoralists across the super continent, the Eurasian steppe belt has been used to explain the initial migrations of pastoralist communities into Central Asia during the Eneolithic (ca. 3300 cal BC), known as the "Afanasievo", from eastern European "Yamnaya" communities^{17,18}. Limited human population genetic data appears to support such west-east movements, including gene flows in the opposite direction¹⁹, which are also associated with later expansions of bronze metallurgical economies up to the first millennium BC²⁰ and also Iron Age (ca. 500 cal BC), horse-mounted cultures known as the "Scythians"^{21,22}.

The second hypothesis applies a similar ecological framework but draws a vector of cultural transmission from the Near East to Central Asia via a near continuous series of foothill zones from the Pamir to Altai Mountains, dubbed the "Inner Asian Mountain Corridor" (IAMC)²³. Along these lines, pastoralists are thought to have spread into Central Asia during the fourth millennium BC by exploiting seasonal rhythms of vegetation growth along montane elevational gradients in order to provide graze for livestock²⁴. The distinct pathways of these two proposed routes, one via Europe and the other more directly from the Near East, provides a basis to examine the mitochondrial diversity of goats in order to reconstruct the spread of herding economies into Central Asia and later genetic flows of goats across the region²⁵. To date, a very limited number of ancient mtDNA sequences have been analyzed, which only represent Neolithic Europe²⁶ and the Near East^{27–29} and also Iron Age China^{30,31}.

Here, we analyze the hypervariable region I of the control region and cytochrome *b* of the mitochondrial genome of goats recovered from Bronze and Iron Age sites located along the Eurasian steppe belt and IAMC. Control region sequences of mtDNA contain high rates of polymorphisms that characterize particular haplogroups, while as a whole, mtDNA is maternally inherited, does not recombine, and is present in high frequencies relative to nuclear DNA, thus serving as an easily recoverable genetic tracer of ancestry. As a coding region of mtDNA that is highly conserved, cytochrome *b* sequences generally reflect inter-specific variation, which we use here to differentiate between domesticated sheep and goat, in addition to wild *Capra* species³². Siberian ibex (*Capra sibirica*) are currently the only wild goat species endemic to the mountainous regions of Central Asia and Mongolia, which are present in the zooarchaeological assemblages of sampled sites in this study. There is the possibility that ancient distributions of wild goats were different in the past than present, which may have included the markhor (*Capra falconeri*) that is currently endemic to Tajikistan, northern Afghanistan, and western Tibet³³.

Sampled sites in the IAMC

Begash. Currently, the best documented settlement site in Kazakhstan is Begash. The site is located at about 800 m.a.s.l. in a tributary river valley of the Koksu River in southeastern Kazakhstan. Occupations at the site by pastoralists began at least by 2400 cal BC and reflect a near continuous use of the settlement with small intermittent gaps up to the early 20th century, which is supported by a robust radiocarbon chronology of 35 AMS radiocarbon dates^{34,35}. Recovered architecture includes low-lying, rectangular stone foundations, over which organic material, likely animal hides or felt, was pitched to form small tent-like dwellings³⁴. The faunal assemblage from the site consists largely of domesticated sheep/goat and cattle throughout the cultural sequence, while horses were recovered in small numbers from layers dated to the early second millennium BC and subsequent periods, indicating the development of herding domesticated bovids at the site in the third millennium BC may have occurred without horse riding³⁶. Macrobotanical remains recovered from the site demonstrate the presence of domesticated wheat, barley, and broomcorn millet in low frequencies since the second half of the third millennium BC, but these remains were highly concentrated in a human burial cist and do not inform on the economic use of these crops^{13,35}. Stable isotopic research on livestock skeletal remains indicates livestock were foddered with millet byproducts, implying a substantial

investment in agriculture by 2500 cal BC (Hermes et al., forthcoming). Bronze pins and other small implements were also recovered from second millennium layers of the site³⁴.

Tasbas. The settlement site of Tasbas is located at about 1500 m.a.s.l. on the Bayan-Zherek plateau of the Dzhungar Mountains in eastern Kazakhstan. The earliest phase of the site began at about 2800 cal BC, but is solely represented by a similar human cremation cist to that at Begash, in which domesticated wheat grains were recovered and directly dated to about 2500 cal BC³⁷. The site appears to have been abandoned until the late second millennium BC³⁷, when a complex agricultural economy then characterized the subsistence economy, indicated by local cultivation and processing of barley, wheat, millets, and legumes³⁸, in addition to abundant skeletal remains of domesticated livestock³⁷. The site remained in use until the Final Bronze Age (ca. 800 cal BC).

Dali. Located about 1 km away from Tasbas, Dali contains evidence of intensive occupation by pastoralist communities in the first half of the third millennium BC, which is represented by a larger area of recovered living surfaces and greater number of ceramic material and faunal skeletal remains (Frachetti et al., forthcoming). Architecture of the early phase of Dali comprises pit-house structures that are lined by small boulders, and numerous post-holes indicate the likelihood of pitching tents above the subterranean dwellings. Similar to Begash, domesticated sheep/goat and cattle were foddered with millet during this early phase of the site, reflected the earliest evidence for agriculture in the eastern steppe region (Hermes et al., forthcoming). The second phase of Dali began by 1800 cal BC after a hiatus in occupation, and the site appears to have been abandoned by 1400 cal BC. In both phases of the site, there is evidence of bronze production, represented by copper ores and finished bronze implements, including jewelry and utilitarian pins.

Uch-Kurbu. Located at 1750 m.a.s.l. in the Tian Shan mountains of Kyrgyzstan, Uch-Kurbu is still actively under archaeological investigation, but preliminary results indicate late Bronze Age occupations by mobile pastoralists who were also engaged in millet cultivation (Motuzaite-Matuzeviciute et al., forthcoming). The site largely consists of Bronze Age human burials with associated ritual pits that date to about 1700-1300 cal BC. Occupations at the site likely extended into the early Iron Age.

Sampled sites in the "Eurasian Steppe Belt"

Bozshakol. The settlement of Bozshakol dates to the late Bronze Age and also functioned as a large-scale metallurgical complex (Dimitry Voyakin, personal communication & unpublished report). A series of unpublished radiocarbon dates indicate the site was occupied from about 1450-1220 cal BC. The faunal assemblage at the site consists largely of domesticated sheep/goat and cattle, but these materials have not been formally analyzed

Taldysai. The settlement of Taldysai dates to the middle-late Bronze Age and, like Bozshakol, also functioned as a large-scale metallurgical production complex (Antonina Erlomaeva, personal communication). Complex smelting pits with long air channels were recovered throughout the site, in addition to numerous ores, slags, and finished bronze objects. A series of unpublished radiocarbon dates indicate the site was in use from about 1900 to 1400 cal BC, which appears to be divided into earlier and later phases. Excavations at the site produced a rich assemblage of faunal skeletal remains, which suggest a subsistence economy focused on sheep/goat and cattle pastoralism, but these materials have not been formally analyzed.

Results and Discussion

Capra hircus mtDNA Recovery. Two separate mtDNA sequences, 193-bp of the control region and 110-bp of cytochrome b, were successfully amplified and sequenced for 20 of 41 ancient samples that were identified as probable domesticated goat (Table 1). One specimen failed to generate the 193-bp amplicon but yielded a 130-bp sequence overlapping with diagnostic loci of the control region using different primers (Table S1). Although the primers used to amplify sequences of the control region

are generally *Capra*-specific, one sample produced a sequence from *Ovis aries*, which was the only sample from Taldysai to result in a control region sequence. Nine samples only yielded cytochrome *b* sequences, which revealed that seven samples were from *Ovis aries*, while the remaining two were from *Capra hircus* (Table S2). Ten samples failed to amplify sequences of the control region or cytochrome *b* (Table S3). Results were confirmed with duplicates taken from independent DNA extractions of each sample. The high rate of success (63%) in amplifying a relatively long fragment of the control region (193-bp) in specimens confirmed as *Capra* spp. indicates good preservation of ancient DNA in the samples, which likely reflects the generally cool continental climate of Inner Asia and high-elevation of sampled sites. The success rate was higher (75%), if only considering cytochrome *b* sequences irrespective of taxon.

Capra hircus mtDNA Diversity. Taken together, the ancient sequences represent divergent mtDNA lineages of Capra hircus that correspond to haplogroups A, C, and D (Table 1), which are well characterized based on modern datasets consisting of more than 3000 domesticated and wild goats^{9,11,12}. Using GenBank BLAST searches, 10 out of 21 Capra sequences of the control region were found to be previously undocumented, which included four haplotypes of lineage D and one haplotype of lineage C. The late Bronze Age (ca. 1600-1000 cal BC) is best represented in our sample (n = 12), followed by the early-middle Bronze Age (ca. 2700-1600 cal BC; n = 4) and the Iron Age (ca. 400-20 cal BC; n = 2).

Diversity of mtDNA haplotypes was lowest for the late Bronze Age site of Bozshakol in northern Kazakhstan, indicated by five sequences of different individuals that belong to haplogroup A (Fig. 1), three of which were identical. Notably, mitochondrial diversity was higher in the IAMC (Fig. 1), as indicated by sequences categorized as haplogroups A (n = 8), D (n = 4), and C (n = 2). IAMC sequences were unique to one another, confirming the sampling of different individuals that could not be confidently known *a priori* based on varied skeletal elements. Sequences of domesticated goat recovered from Dali, representing the earliest pastoralist occupations in our study, belong to haplogroup A (n = 4), while late Bronze Age and Iron Age layers of IAMC sites contained an unexpectedly high ratio of C and D haplotypes to A haplotypes (6:5). This distribution may indicate an influx of goats with diverse maternal origins into the IAMC after the middle Bronze Age. Although the sample size for the Iron Age is small, two out of three sequences are of lineage D, suggesting mtDNA diversity, reflected by frequencies of rare haplotypes, may have increased up to the end of the first century BC.

Sequences representing haplogroups B, G, or F were not recovered in this study. We did not expect to identify G or F haplotypes, since domesticated goats of the G lineage are largely restricted to northern and central Africa and have a modern global frequency of 0.9%, while the F lineage is rarest of all, having only been isolated in three Sicilian domesticated goats⁹. However, we thought it would be likely to find B haplotypes in Central Asian goats, since B haplotypes are the second most abundant in modern distributions (ca. 6.5%)^{9,11}, and two B haplotypes were found in Iron Age goats from northern China³⁰. Goats of lineage B were likely to have passed through Central Asia during their spread into east Asia. Previously, it was thought that goats representing a B sub-lineage were independently domesticated in China based on intra-haplogroup genetic distances³⁹, but this was shown to be incorrect after ancestral B lineages were isolated in bezoars¹⁰. This is further supported by coalescent time estimates of lineages based on mtDNA protein-encoding genes, which indicate that the most recent divergence between the A and D lineages dates to 200,000 years ago⁴⁰. Nevertheless, the original claim of Chinese goat domestication remains implausible since bezoars, the wild ancestors of domesticated goats, have not been identified in east Asia⁴¹. The absence of B haplotypes in our sample is likely an anomaly of sample size.

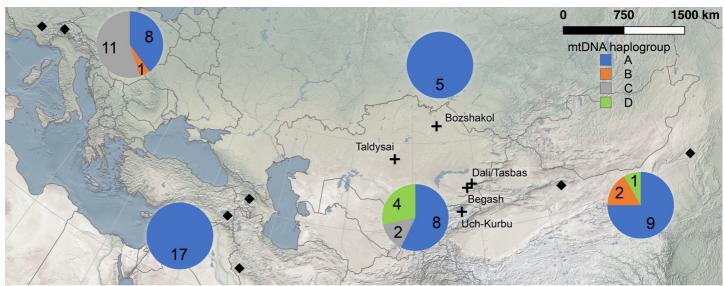


Figure 1: Map showing ancient frequencies of *Capra hircus* mtDNA haplogroups across Eurasia. Sites analyzed in this study are indicated by crosses, and sites previously published are indicated by rhombuses.

Phylogenetic Analysis of *Capra hircus* **across Eurasia.** A neighbor-joining phylogenetic tree was constructed with ancient goat mtDNA haplotypes from Central Asia and those previously analyzed from the Near East^{27–29}, Europe^{26,42}, and northern China^{30,31}, in addition to modern sequences (Fig. 2; Tables S4-5). Ancient sequences from Europe and the Near East represent Neolithic goats (ca. 8000-3000 cal BC), which predate the goats in this study and serve as an ancestral source for tracing A lineages across Eurasia, while sequences from northern China represent the Iron Age (ca. 500 cal BC).

The oldest goat sequence in our sample (Dal-EBA-1) was recovered from the early Bronze Age phase of Dali (ca. 2700-2500 cal BC) in the IAMC (Fig. 1), which clusters with sequences from the Pre-Pottery Neolithic in western Iran and Iron Age in China as a subclade of lineage A (Fig. 2, clade 1). These genetic relationships possibly indicate that the first wave of domesticated goats spreading into eastern Kazakhstan were drawn from an Iranian genetic pool, which then reached east Asia by the Iron Age. An additional west-to-east flow of goat lineages is indicated by Iron Age Chinese goat sequences in haplogroup A that cluster with sequences from both Bozshakol and sites in the IAMC (Fig. 2, clade 2). This implies that the spread of goat lineages into China may be traced through both the northern steppe region via the Altai mountains and Mongolia and from the IAMC. However, Central Asian ancient goat sequences are scattered throughout the A clade, which is likely an outcome of A haplotypes being the most dominant in domesticated goats after large population expansions of A groups since domestication 10,11. Thus, it remains difficult to isolate a specific geographic vector of goats moving into China via Central Asia without substantially larger datasets.

Unexpectedly, two out of the four D haplotypes from goats in the IAMC during the Bronze and Iron Ages belong to a newly discovered sister clade to previously known D haplotypes (Fig. 2, clade 3). This result suggests a degree of genetic continuity in domesticated goats at Begash from 1600 to 20 cal BC. Interestingly, no modern descendant or closely related sequences of this lineage are known to exist, indicating that this mtDNA line likely died out from reasons that remain unclear. Haplotypes of lineage D are exceedingly rare in contemporary world-wide distributions $(0.6\%)^{9,11}$, but are more common in bezoar populations on the Iranian plateau (ca. 13%)⁹. Previously, one D haplotype was identified from Iron Age northern China³⁰, which clusters with the other two Bronze and Iron Age haplotypes from the IAMC on the main D clade, including two modern D haplotypes from Kyrgyzstan (Fig. 2). Thus, ancient frequencies of D haplotypes were likely far higher in Central Asia than in the present.

Two haplotypes of the C lineage were recovered from sites in IAMC during the late Bronze Age (Fig. 2), which tightly cluster with and are ancestral to C haplotypes that were recovered from Neolithic southern France (Fig. 2). It is possible that the first wave of domesticated goats into Europe reflects a bifurcation of the C lineage from its source in the Near East, while a more ancestral lineage contributed to the genetic pool that spread into Central Asia. Haplotypes of lineage C are similarly rare in contemporary global distributions (1.4%) and are higher in bezoar populations (ca. 40%)⁹. While we lack a diachronic view of C haplotypes in the IAMC, the presence of this lineage further

indicates high mtDNA diversity of goats in the mountain regions of Central Asia compared to the northern steppe zone that is suggestive of different intensities of social interaction that may characterize these regions.

Due to genetic drift ultimately leading to monomorhism, a single lineage should become dominant in a diverse population after 4*N_{ef} generations, where N_{ef} represents the effective number of females^{43,44}. Goat skeletal remains are about ten times more infrequent than those of sheep and about five times as infrequent as cattle remains from sites in the IAMC during the Bronze and Iron Ages^{36,37,45}, indicating that goat population sizes were relatively small compared to other domesticated taxa. Without a large population to buffer the effects of genetic drift, the persistence of C and D lineages in goats is likely due to high-rates of gene flow along the IAMC, perhaps after a diverse founding population settled in the region. Frequent breeding events could have linked discrete goat populations of pastoralist communities as a large, global effective population, thus maintaining the prevalence of rare mtDNA lineages. A high degree of social interaction, likely driven by both seasonal migrations of mobile pastoralists^{16,23,24} and sprawling economic networks for the mining and exchange of copper and tin to produce bronzes during the late Bronze Age and Iron Age^{20,46–48}, remains a strong candidate for promoting inter-regional gene flow among livestock.

Given the level of economic activity previously identified archaeologically among ancient steppe pastoralist communities^{49–52}, it may be possible to recover evidence of deliberate goat breeding in order to suit economic needs, which may have paralleled the geographic scale and social intensity of other interaction networks. Adaptations to cold temperatures and high-altitude, in addition to greater endurance for moving long distances during migrations, would benefit pastoralists utilizing the resources of the IAMC and beyond. Traits that would enhance the production of milk and wool as secondary products, especially through the harsh seasonal environment of Inner Asia, would have likely been under strong selection pressure. In contemporary breeds, mutations in the goat α_{s1} casein gene (CSN1S1) are well characterized^{53,54}, which have effects ranging from increasing casein synthesis to yield concentrations of 3.6 g/L to no production of casein by goats with a homozygous null allele^{55–57}. The effect on lipid composition of goat milk has only recently been genetically characterized, which identified a number of loci linked to overall lipid amount and the relative proportions of unsaturated and saturated fatty acids⁵⁴. The genetic history of goat, sheep, and cattle likely produced rich evidence of human action. Indeed, recent genetic research on Bronze and Iron Age domesticated horses from north-eastern Kazakhstan demonstrates that pastoralist communities made breed improvements to increase milk production, minimize body water loss in arid environments, and boost running speed, while also carefully preventing inbreeding⁵⁸. While goats are not typically considered to be a high-value animal that conveys wealth and power, such as horses, it remains to be determined whether similar selective pressures were applied to improve food or fiber production, enhance herd security, or serve particular cultural preferences surrounding animals reasons that can convey significant social force.

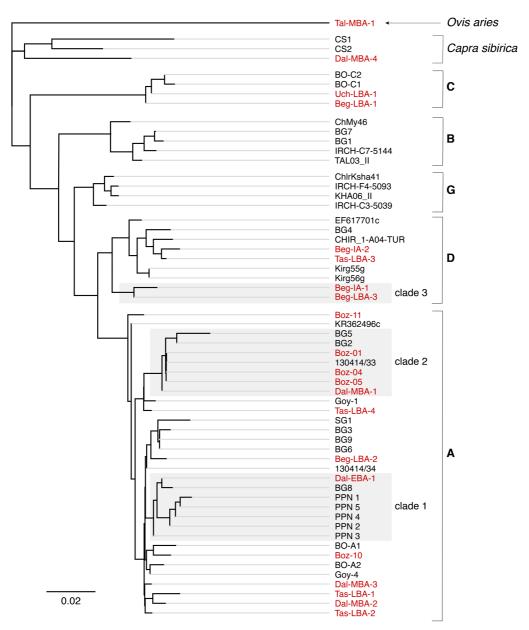


Figure 2: Neighbor-joining phylogenetic tree using Tamura-Nei genetic distance model of ancient mtDNA sequences (HVRI and Cytb regions) identified in this study (red), in addition to previously published ancient and contemporary reference sequences from Eurasia; *Ovis aries* was used as the outgroup. Haplogroup designations of *Capra hircus* are listed to the right of the sample ID numbers. Highlighted clades 1-3 are discussed in the text. The clade of *Capra sibirica* exhibited a "Mr. Bayes" posterior probability of 100% for the sister clade of sequence Dal-MBA-4 to sequences CS1 and CS2.

Capra sibirica or Ovis Aries? A preliminary objective of this research was to define the mitochondrial diversity of Siberian ibex (Capra sibirica), which remains under-characterized in currently known and ancient biogeographic distributions 41,59-62. We further sought to explore the potential for introgression between domesticated and wild goats. Surprisingly, two specimens from Begash previously identified as Siberian ibex based on zooarchaeological criteria were determined to be domesticated sheep, indicated by cytochrome b sequences that are specific to Ovis aries (Table S2). Two additional Siberian ibex specimens did not yield amplicons, likely due to DNA damage resulting from burning that left traces on bone surfaces. One Siberian ibex specimen from Dali dating to the middle Bronze Age (ca. 1800-1500 cal BC), which was identified based on more reliable cranial morphology, produced Capra sibirica sequences of both the control region and cytochrome b. While primer pairs that were used for domesticated goats were also used for Capra sibirica specimens, an additional pair of primers were designed that successfully amplified a fragment of the control region that overlapped on the 5' end of the 193-bp amplicon, resulting in a final control region sequence of 221-bp. This sequence phylogenetically clustered as a sister group to previously published modern Capra sibirica sequences, which is supported by a "Mr. Bayes" 100% posterior

probability (Fig. 2). To date, these sequences represent the only ancient DNA recovered from *Capra sibirica* and demonstrate a newly discovered degree of genetic diversity in this taxon.

The misidentification of *Capra sibirica* demands that new criteria be developed to determine the morphological distinction of this wild goat species. Currently, this problem impacts the understanding of hunting Siberian ibex by ancient pastoralists in Central Asia, which was likely less common than previously suggested³⁶. If it turns out that more *Capra sibirica* specimens are, in fact, domesticated sheep, then the relative importance of hunting in pastoralists economies needs to be reevaluated. In general, morphological criteria used to identify Central Asian domesticated and wild taxa are borrowed those developed for European and Near Eastern populations, which can lead to ambiguity in taxonomic identifications (Cheryl Makarewicz, personal communication). It is probable that identifications of other taxa may be affected given the finding that domesticated sheep were mistaken for Siberian ibex. Due to a high diversity of wild ungulate species in Central Asia, this issue requires careful attention.

At Begash, for example, Central Asian red deer (Cervus elaphus ssp.) are the most abundant wild prey in the faunal assemblage from all time periods³⁶, but this taxon may comprise several Cervus species and subspecies, including Yarkand deer (Cervus elaphus yarkandensis), Bactrian deer (Cervus elaphus bactrianus), and Tian Shan wapiti (Cervus canadensis ssp.). While a small number of studies have identified genetic distinctions among these taxa^{63,64}, ancient biogeographical distributions remain under-characterized. Each of these taxa are associated with distinct ecologies and behaviors⁶⁵, which impact how humans search for and ultimately harvest prey. Furthermore, Argali sheep (Ovis ammon) were also recovered from Begash as the third most abundant wild taxon³⁶, but these identifications may be questionable and should be revisited with aDNA approaches. While proteomic analysis of collagen peptides (ZooMS) may be used to differentiate sheep from goat specimens as a relatively cheap biomolecular method, this technique is less sensitive within genera, especially for Capra⁶⁶ but likely for Cervus and Ovis as well. Thus, aDNA may provide robust identifications of wild prey, while generating informative data of genetic variability through time⁶⁷. These datasets would be valuable for understanding how Mesolithic and Neolithic hunter-gatherer communities in the IAMC exploited the landscape for high-valued prey by targeting ecological niches of particular wild ungulates^{68–71}. This line of inquiry remains unexplored but is relevant for understanding subsistence economies that existed before the spread of domesticated livestock to Central Asia and the transformations in food production that followed.

Conclusions

Despite small sample sizes, the results of this study are suggestive of higher levels of gene flow among domesticated goats along the IAMC, which is likely a reflection of increased social interaction in the foothill zones, compared to the open steppe landscape. The northern "Eurasian steppe belt" is typically viewed as metaphorical highway of cultural interaction between eastern Europe and Siberia, which is thought to be associated with the spread of pastoralism to the Altai Mountains via migrations of Afanasievo communities¹⁷. A recent genome-wide analysis of humans, including those associated with the Afanasievo and purported antecedent Yamnaya cultural horizons, implies that such migrations may have taken place¹⁹. Later Iron Age human populations further display genetic clines along this steppe belt zone, indicating prevalent admixture between east and west communities^{21,22}. However, this genetic pattern may be a result of earlier genetic patterns that were present since the Neolithic, since samples from this time period have yet to be analyzed, while human samples, in general, from southern Central Asia are further lacking. Thus, inferences of human mobility and admixture along the steppe belt zone may be an artifact of geographic sampling bias. Based on the low mtDNA diversity present in late Bronze Age domesticated goats in the "Eurasian steppe belt." there may be an unexpectedly low degree of admixture among northern steppe communities. The goats analyzed here appears to be a founder population that was present in eastern Europe after an earlier translocation of domesticated goats with A haplotypes from the Near East via the Caucasus.

In the IAMC, we observed a possible shift in the frequencies of mtDNA lineages from the early-middle Bronze Age (2700-1600 cal BC) to the late Bronze Age and Iron Age (1600-20 cal BC), which may be a result of reconfigured socio-economic networks that facilitated transfers of goats belonging to C and D lineages to the region from diverse genetic pools in the Iranian plateau. In the absence of individual animals moving long distances along the IAMC, genetic isolation between

discrete goat populations may have been greatly diminished due to directed breeding patterns of goats by pastoralists communities that effectively created a macro-population of goats that maintained diverse maternal lineages. This implies that Bronze and Iron Age pastoralists may have cultivated multiple breeds carrying valuable genetic resources. These findings provide additional support that the IAMC was a dynamic locus of cultural activity spanning distant regions of Central Asia²³.

More research is needed to resolve the precise nature of livestock translocations, interregional genetic networks, and selective pressures on livestock. This study offers a much-needed expansion of datasets for characterizing ancient goat mitochondrial diversity in Eurasia, and larger sample sizes spanning more sites along proposed transmission routes will improve the quality of inferences that can be drawn from maternal lineages. The addition of other domesticated taxa, such as sheep and cattle, to future aDNA analysis will help clarify differences in genetic sourcing from various geographical regions. Livestock taxa may not have tracked one another during the initial spread of pastoralist economies into Central Asia, and genetic variability in livestock has the potential to be a novel means for resolving social connectivity and mobility among pastoralist communities. By also examining genetic variability in wild taxa, ancient biogeographic patterns of may be identified to reconstruct a more complete picture of human engagements the landscape that may further reveal nuances in the relationship between hunting and herding strategies.

While the PCR-based approach used in this study is effective for targeting specific sequences that are relatively short (< 200-bp), especially of highly abundant mtDNA in skeletal remains, studying genetic variability in the nuclear genome is essential for understanding individual phenotypes, selection pressures, and admixture between populations. Analyses of increased genetic coverage in both the mitochondrial and nuclear genomes through aDNA enrichment and high-throughput sequencing⁷² will vastly improve inferences about the initial movement of domesticated livestock into Central Asia and farther east into Siberia and China.

Methods

aDNA quality control. Laboratory work in this study was conducted in the Ancient DNA Laboratory of Kiel University following established protocols^{73–75}. Three separate rooms were utilized each for sample preparation, pre-PCR setup, and PCR reactions. Contamination control included strict access to zooarchaeological materials and aDNA samples, wearing of coveralls, hoods, masks, and gloves, using of positive air-flow PCR workstations, irradiating workspaces, laboratory consumables, utensils, and pipettes with ultraviolet light, and using of sterile RNA/DNA-free plasticware and filter tips. Negative controls were employed during DNA extraction and PCR preparation that were also analyzed for amplicons in order to rule out experimental contamination.

Sample selection, preparation, and DNA extraction. Bones and teeth from 42 probable goats, identified by morphological features 76,77 and a subset of these by the proteomic analysis known as zooarchaeology by mass spectrometry (ZooMS) 66 , were sampled from six archaeological sites with Bronze and/or Iron Age occupations in Kazakhstan and Kyrgyzstan (Table 1,S2-3). Samples were soaked in 100% bleach solution for 5 min in order to remove external contamination, followed by a soaking for 5 min and two rinses with ddH₂O. Samples were ground to a fine powder with a ball mill and digested in ca. 500 μ L 0.5 M EDTA (pH 8.0) and 20 μ L proteinase K (25 mg/mL) overnight at 37°C. DNA was extracted with a large-volume extraction protocol using a guanidinium-silica based method⁷⁸. Two independent DNA extractions were performed for each sample.

mtDNA sequence analysis. Two loci in mtDNA were amplified using primers specific to the *Capra* genus: a 193-bp fragment in the control region containing diagnostic polymorphisms for determining haplogroups and haplotypes and a 110-bp fragment in cytochrome *b* for species identification. Amplifications were performed as singleplex PCRs in a final volume of 25 μL (Table S4). Reactions were performed in a Mastercycler (Eppendorf) with the following conditions: initialization at 94°C for 10 min, 42 cycles of 94°C for 30 s, 50-60°C for 30 s (primer dependent, see (Table S1), 72°C for 30 s, and a final elongation step at 72°C for 10 min. The quality of PCR products was checked on a QIAxcel system, and those with single bands of expected size were subjected to direct sequencing with the BigDye Terminator v3.1 Kit (Applied Biosystems), following the instructions of the

manufacturer. Sequencing products were purified applying the DyeEx 2.0 Spin Kit (Qiagen) and analyzed using the ABI Prism 310 and 3130 Genetic Analyzers (Applied Biosystems).

Phylogenetic analysis. Ancient control region and chytochrome b sequences were concatenated for each sample, resulting in a total sequence length of 303-bp. Sequences were pair-wise aligned to one another in addition to 23 previously published ancient sequences (Table S4) and 14 modern sequences of Capra spp. (Table S5). In cases where reference sequences of the control region were not associated sequences of cytochrome b, we used cytochrome b sequences from sample KG170121 as a "dummy" sequence. This approach is justified because of very low genetic variation in cytochrome b sequences for each Capra spp., which mainly served to improve phylogenetic clustering of Siberian ibex away from domesticated goats. Aligned sequences were trimmed so modern reference sequences, which were taken from complete mitochondrial genomes, were the same length as sample sequences. However, most ancient sequences were shorter than sampled sequences due to different primers used in those studies. A neighbor-joining tree using the Tamura-Nei genetic distance model was constructed in Geneious v. 10.0.7 with the Ovis aries sample as an outgroup. Additionally, a phylogenetic tree was constructed using MrBayes v. 3.2.6, which provides Bayesian posterior probability estimates of tree branches⁷⁹. The simulation was set using the JC69 substitution model, invgamma rate variation, four gamma categories, and Ovis aries as an outgroup; MCMC chain length was set to 200,000 with a sampling frequency of 200 and burn-in of 50,000.

Data availability. Genetic sequences recovered from this study are provided in Tables S7-8.

Acknowledgements

We thank Alexander Flache and Kim Callan for assisting in laboratory work. Thanks are also due to Lisa Bömhe for help facilitating the start of this research. Thank you to Mike Buckley for collaboration on ZooMS. Finally, we thank the Institute of Clinical Molecular Biology in Kiel for providing Sanger sequencing as supported in part by the DFG Cluster of Excellence "Inflammation at Interfaces" and "Future Ocean". We thank the technicians T. Naujoks and C. Noack for technical support.

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Table 1: Samples that produced amplicons in the control region and cytochrome b.

Gen_ID	Old_ID	New_ID	Site	Period	Chronology	Zooarch Taxon	Skeletal tissue	Skeletal element	Direct date	Genetic Taxon (cyt b)	Haplogroup	Unique haplotype
KG160125	T068	Beg-LBA-2	Begash	Iron Age	390 cal BC-AD 30	Capra hircus	tooth	dp/4		Capra hircus	Α	X
KG160130	T067	Beg-IA-1	Begash	Iron Age	390 cal BC-AD 30	Capra hircus	tooth	P/4		Capra hircus	D	X
KG170136	BG0294	Beg-IA-2	Begash	Iron Age	390 cal BC-AD 30	Capra hircus	bone	humerus		Capra hircus	D	X
KG160136	T062	Beg-LBA-3	Begash	Late Bronze Age	1625-1000 cal BC	Capra hircus	tooth	dp/4		Capra hircus	D	X
KG170117	BG0185	Beg-LBA-1	Begash	Late Bronze Age	1625-1000 cal BC	Capra hircus	bone	p1		Capra hircus	С	X
KG170116	Boz-11	Boz-11	Bozshakol	Late Bronze Age	1450-1220 cal BC	Caprine	bone	parietal		Capra hircus	Α	X
KG170120	Boz-01	Boz-01	Bozshakol	Late Bronze Age	1450-1220 cal BC	Caprine	tooth	P/4		Capra hircus	Α	
KG170121	Boz-05	Boz-05	Bozshakol	Late Bronze Age	1450-1220 cal BC	Caprine	tooth	P/3		Capra hircus	Α	
KG170122	Boz-04	Boz-04	Bozshakol	Late Bronze Age	1450-1220 cal BC	Caprine	tooth	P/3	X	Capra hircus	Α	
KG170128	Boz-10	Boz-10	Bozshakol	Late Bronze Age	1450-1220 cal BC	Caprine	bone	parietal		Capra hircus	Α	X
KG160131	T060	Dal-EBA-1	Dali	Early Bronze Age	2880-2150 cal BC	Capra hircus	tooth	dp/4		Capra hircus	Α	
KG160126	T051	Dal-MBA-1	Dali	Middle Bronze Age	1810-1470 cal BC	Capra hircus	tooth	P/4		Capra hircus	Α	
KG160132	T047	Dal-MBA-2	Dali	Middle Bronze Age	1810-1470 cal BC	Capra hircus	bone	horn core		Capra hircus	Α	
KG160134	T061	Dal-MBA-3	Dali	Middle Bronze Age	1810-1470 cal BC	Capra hircus	tooth	dp/4		Capra hircus	Α	
KG160137	OP3-SKF1	Dal-MBA-4	Dali	Middle Bronze Age	1810-1470 cal BC	Capra sibirica	bone	petrous		Capra sibirica	SIBIRICA	X
KG170127	TS-18	Tal-MBA-1	Taldy-Sai	Middle Bronze Age	1640-1340 cal BC	Caprine	tooth	P/4		Ovis aries	OVIS	
KG160127	T066	Tas-LBA-1	Tasbas	Late Bronze Age	930-806 cal BC	Capra hircus	tooth	P/4		Capra hircus	Α	
KG160129	T055	Tas-LBA-2	Tasbas	Late Bronze Age	1208-1054 cal BC	Capra hircus	tooth	P/4		Capra hircus	Α	X
KG160133	T046	Tas-LBA-3	Tasbas	Late Bronze Age	1208-1054 cal BC	Capra hircus	bone	horn core		Capra hircus	D	X
KG160135	T065	Tas-LBA-4	Tasbas	Late Bronze Age	1208-1054 cal BC	Capra hircus	tooth	P/3		Capra hircus	Α	
KG170131	UK-01	Uch-LBA-1	Uch-Kurbu	Late Bronze Age	1200-905 cal BC	Capra hircus	tooth	dp/4		Capra hircus	С	

Table S1: Primers used to amplify loci in Capra mtDNA

Primer Pair	Primer ID	Sequence (5' to 3' direction)	Taxon	Locus	Amplicon length	Annealing Temperature	Reference
G1	CAP-FII	GATCTTCCYCATGCATATAAGCA	Capra spp.	HVRI	130 bp	55°C	26
O1	CAP-RII	CGGGTTGCTGGTTTCAC	Capra spp.	HVRI	100 55	00 0	26 26
G2	CapFC1	CTCTGTAACTCACATTTGTC	Bovidae	Cytb	110 bp	50°C	26
OL.	CapRB1b	GTTTCATGTTTCTAGAAAGGT	Bovidae	Cytb			26
G3	CAP-FII	GATCTTCCYCATGCATATAAGCA	Capra spp.	HVRI	193bp	55°C	29
•	CAP-RIII	GATAAAGTTCATTAAATAGCTAC	Capra spp.	HVRI			
G4	CSib-FI	AACATGCGTATCCCGTCCAC	Capra sibirica	HVRI	120 bp	60°C	This study
	CSib-RI	GGCCCTGAAGAAGAACCAG	Capra sibirica	HVRI			This study

Table S2: Samples that only produced amplicons in cytochrome b.

Gen_ID KG170112	Old_ID BG0084	Site Begash	Period Middle Bronze Age	Chronology 1940-1740 cal BC	Zooarch Taxon Capra hircus	Skeletal tissue bone	Skeletal element radius	Genetic Taxon (cyt b) Ovis aries
KG170112 KG170113	T053	Dali	Early Bronze Age	2880-2150 cal BC	Capra riricus Caprine	tooth	P/3	Ovis aries
KG170113	TS-06	Taldv-Sai	Late Bronze Age	1640-1340 cal BC	Caprine	tooth	M/1	Ovis aries
KG170118	TC-19	Taldy-Sai	Late Bronze Age	1640-1340 cal BC	Caprine	tooth	P/3	Ovis aries
KG160128	T039	Tasbas	Late Bronze Age	1416-1287 cal BC	Caprine	tooth	P/3	Ovis aries
KG170129	BG0100	Begash	Middle Bronze Age	1940-1740 cal BC	Capra hircus	bone	ulna	Capra hircus
KG170130	BG0145	Begash	Late Bronze Age	1625-1000 cal BC	Capra hircus	bone	p1	Capra hircus
KG170137	BG0376	Begash	Late Medieval Period	cal AD 1260-1410	Capra sibirica	bone	astragalus	Ovis aries
KG170139	BG0206	Begash	early Iron Age	970-400 cal BC	Capra sibirica	bone	cervical vert	Ovis aries

Table S3: Samples that failed to produce amplicons.

Gen_ID	Old_ID	Site	Period	Chronology	Zooarch Taxon	Skeletal tissue	Skeletal element
KG170115	Boz-03	Bozshakol	Late Bronze Age	1450-1220 cal BC	caprine	tooth	P/3
KG170119	TC-21	Taldy-Sai	Late Bronze Age	1640-1340 cal BC	Caprine	tooth	P/4
KG170123	BG0113	Begash	Middle Bronze Age	1940-1740 cal BC	Capra hircus	bone	horn core
KG170125	TS-20	Taldy-Sai	Late Bronze Age	1640-1340 cal BC	Caprine	tooth	M/3
KG170126	TS-22	Taldy-Sai	Late Bronze Age	1640-1340 cal BC	Caprine	tooth	P/4
KG170132	T001	Begash	Middle Bronze Age	1940-1740 cal BC	Caprine	tooth	M/3
KG170133	T002b	Begash	Middle Bronze Age	1940-1740 cal BC	Caprine	tooth	P/3
KG170135	BG0200	Begash	Early Iron Age	970-400 cal BC	Capra sibirica	bone	p1
KG170138	BG0141	Begash	Late Bronze Age	1625-1000 cal BC	Capra hircus	bone	astragalus
KG170140	BG0442	Begash	Historic Period	cal AD 1680-1900	Capra sibirica	bone	calcaneus

Table S4: Ancient reference Capra hircus haplotypes

Sample ID	Country	Chronology	Haplogroup	Genbank	Reference
BO-A1	France	5100 cal BC	Α	DQ847510 + DQ847506	26
BO-A2	France	5100 cal BC	Α	DQ847510 + DQ847507	26
BO-C1	France	5100 cal BC	С	DQ847511 + DQ847508	26
BO-C2	France	5100 cal BC	С	DQ847511 + DQ847509	26
BG6	China	ca. 500 BC	Α	GU356623	30
BG1	China	ca. 500 BC	В	GU356624	30
BG4	China	ca. 500 BC	D	GU356625	30
BG9	China	ca. 500 BC	Α	GU356626	30
BG3	China	ca. 500 BC	Α	GU356627	30
BG5	China	ca. 500 BC	Α	GU356628	30
SG1	China	ca. 500 BC	Α	GU356629	30
BG2	China	ca. 500 BC	Α	GU356630	30
BG8	China	ca. 500 BC	Α	GU356631	30
BG7	China	ca. 500 BC	В	GU356632	30
130414/33	China	ca. 500 BC	Α	KU686190	31
130414/34	China	ca. 500 BC	Α	KU686191	31
Goy-1	Azerbaijan	5500 cal BC	Α	LC050643	27
Goy-4	Azerbaijan	5500 cal BC	Α	LC050644	27
PPN 1	Iran	ca. 8000 BC	Α	KC404854	28
PPN 2	Iran	ca. 8000 BC	Α	KC404855	28
PPN 3	Iran	ca. 8000 BC	Α	KC404856	28
PPN 4	Iran	ca. 8000 BC	Α	KC404857	28
PPN 5	Iran	ca. 8000 BC	Α	KC404858	28

Table S5: Modern reference Capra haplotypes
Place of Geographic mtDNA Ma

				Place of	Geographic	mtDNA Macro		Complete	
Original Sample ID	Species	Breed	Breed Origin	Collection	Area	Haplo-group	GenBank Acc. Numb.	MtDNA	Citation
CHIR_1-A04-TUR	C. hircus	Turki	Iran	Iran	Middle East	D	KR059502	NO	9
Kirg55g	C. hircus	Kyrgyzstan	Kyrgyzstan	Kyrgyzstan	Central Asia	D	KR059212	YES	9
Kirg56g	C. hircus	Kyrgyzstan	Kyrgyzstan	Kyrgyzstan	Central Asia	D	KR059211	YES	9
ChMy46	C. hircus	Malaysia	Malaysia	Malaysia	East Asia	В	KR059220	YES	9
IRCH-C7-5144	C. hircus	Unknown	Iran	Iran	Middle East	В	KR059703	NO	9
TAL03_II	C. hircus	Taleshi	Iran	Iran	Middle East	В	KR059819	NO	9
ChlrKsha41	C. hircus	Kermanshah	Iran	Iran	Middle East	G	KR059213	YES	9
IRCH-C3-5039	C. hircus	Unknown	Iran	Iran	Middle East	G	KR059216	YES	9
IRCH-F4-5093	C. hircus	Unknown	Iran	Iran	Middle East	G	KR059217	YES	9
KHA06_II	C. hircus	Khalkhali	Iran	Iran	Middle East	G	KR059218	YES	9
CS1	C. sibirica	Wild	-	Russia	Siberia	-	DQ246771 + AJ317874		Unpub. / 12
CS2	C. sibirica	Wild	-	unknown	unknown	-	NC_020626	NO	61
CH101	C. hircus	Pinzgau	Austria	Austria	Europe	D	EF617701	NO	11
BA6	C. hircus	Unknown	Unknown	Egypt	Middle East	Α	KR362496	NO	80

Table S6: PCR setup for mtDNA analysis

Reagent	<u>Volume (μ</u> L)
10x ImmoBuffer (Bioline)	2.5
MgCl ₂ (50 mM)	0.75
dNTPs (each 200 μM)	2
Immolase DNA polymerase (Bioline)	0.2
Primer forward (0.4 µL)	1
Primer reverse (0.4 µL)	1
DMSO	1
Template DNA	1
ddH_2O	15.55

Table S7: Control region sequences recovered from ancient sheep and goat remains.

New_ID Beg-LBA-2	HVRI (G3 primers)
	TGTATAACGCTTCTATCGGCAGTACATAGTACATTTTACTGCATACTCGTACATGGCACATAGGGTCAAATCCATTCTTGCCAACATGCGTATCCCGTCCACTAGGATCACGAGCTTGTTGACCATGCCGCGTGAAACCAGCACCCGCTTGGCAAGGATCCCTCTTCTCGCTCCGGGCCCATTAACCGTGGGG
Beg-IA-1	TGTACAATGTTTCTATCAACAGTACATAGTACATGTACATGTACATGTACATCGGCACATAAAGTCAAATCCGTTCTTGTCAGCATGCGTACCATGCGTACCATGCGACCGGCCCGTTGAAACCAGCAACCCGCTTGGCAAGGATCCCTCTTCTCCGCTCCGGGCCCATTGACCGTGGGG
Beg-IA-2	TGTACAGTATTTCCACCGACAGTACATAGTACATTTTACTGTATATTCGTACATATCGCACATAAAGTCAAATCCGTTCTTGTCAGCATGCGTATCCCGCCCACTAGATCACGAGCTTGTTGACCATGCCGCGCGTGAAACCAGCACCCGCTTGGCAAGGATCCCTCTTCTCGCTCCGGGCCCATTAACCGTGGGG
Beg-LBA-3	TGTACAATGCTTCTATCGACAGTACATTGTACATTTTACTGTATATTCGTACATGCCACATAAAGTCAAATCCGTTCTTGTCAGCATGCGTACCACTAGATCACGAGCTTGTTGACCACTGCCGCGTGAAACCAGCACCCGCTTGACACAGGATCCCTCTTCTCGCTCCGGGCCCATTGACCCTTCGGGA
Beg-LBA-1	TGTACAATATCCCTATCGATAGTACATGGCACATTTTATTGTATACCCGTACATAGCGCATGAAGTCAAAATCCGTCCTCGTCAACATGCATATCCCGTCCACTAGATCACGAGCTTGTTCACCATGCCGCGTGAAACCAGCAACCCGCTTGGCAGGGATCCCTCTTCTCCGCTCCGGGCCCATTAACTGTGGGG
Boz-11	TGTATAATGCTCCTATTGGCAGTACATAGTACATAGTACATTCCTGCATATTCGTACATGGCACATAGAGTCAAATCCATTCTTGTCAACATGCGTATCCCGTCCACTAGATCACGAGCTTGTTGACCATGCCGTCGAAACCAGCAACCCGCTTGGCAGGGATCCCTCTTCTCGCTCCGCGCCCATTAACCGTGGGG
Boz-01	TGTATAATGCTTCTATCAGCAGTACATAGTACATTTTACTGCATATTCGTACATAGCACATAGAGTCAAATCCATCC
Boz-05	TGTATAATGCTTCTATCAGCAGTACATAGTACATTTTACTGCATATTCGTACATAGCACATAGAGTCAAATCCATCC
Boz-04	TGTATAATGCTTCTATCAGCAGTACATAGTACATTTTACTGCATATTCGTACATAGCACATAGAGTCAAATCCATCC
Boz-10	TGTATAATACCTCTATCGGCAGTACATAGTACATTTTACTGCATATTTCGTACATGCCACATGGCACATAGAGTCAAATCCATTCTCGCCAACATGCGTATCCCGTCACTAGATCACGAGCTTGTTGACCATGCCGCGTGAAACCAGCACCCGCTTGGCAGGGATCCCTCTTCTCGCTCCGGGCCCATTAACCGTGGGG
Dal-EBA-1	TGTATAATGCTTCTATTGACAGTACATAGTACATTTTACTGCATATTTCGTACATGCGCACATAGAGTCAAATCCATTCTTGCCAACATGCGTACCACTAGCTCACTAGATCACGAGCTTGTTGACCAGGCGCGTGAAACCAGCAGCCGCTTGGCAGGGGATCCCTCTTCTCGCTCCGGGCCCATTAACCGTGGGG
Dal-MBA-1	TGTATAATGCTTCTATCAGCAGTACATAGTACATAGTACATTTTACTGCATATTCGTACATAGCACATAGAGTCAAATCCATCC
Dal-MBA-2	TGTATAATGCTTCTATCGGCAGTACATAGTACATTTTACTGCATGTTCGTACATGGCACATAGAGTCAAATCCATTCTTGCCAACATGCGTATCCCGTCCATTAGATCACGAGCTTGTTGACCATGCCGC
Dal-MBA-3	TGTATAATGTTTCTATCGGCAGTACATAGTACATTTTACTGCATATTCGTACATGCGCACATAGAGTCAAATCCATTCTTGCCAACATGCGTACCACTAGATCACGAGCTTGTTGACCACTGCGCGCGTGAAACCAGCACCCGCTTGGCAGGGATCCCTCTTCTCGCTCCGGGCCCATTAACCGTGGGG
Dal-MBA-4	TGTACAATCCTTTCACCGATAGTACATAGAACATTCTATTCCATAATCGTACATAATCGTACATAGCACATGAGGTCAAATCTGTTCTTGTCAACGTGCGTACCACTAGATCACGACCATGAGCTTTTTAATCAGACATCACGACCAGCACCCGCTGAAACCAGCACCCGCTCGGCAGGGATCCCTCTTCTCGCTCCGGGCCCCATTAATCGTGGGGGTAGCTATTTAATGAGCTTTTAATGAGCTTTTAATCAGACAT
Tal-MBA-1	TGTACATTTGTTCACTGAAGCACGTAGGGTATTAAACTGCTTGACCGTACATAGTACATGAAGTCAAATCCATTCTAGTCAACATCCGTATCCTGTCCATTAGATCACGAGCTTGTTCACCATGCCGCGTGAAACCAACACCCGCTCAGCAAGGATCCCTCTTCTCGCCTCCGGGCCCATTAACTGTGGGG
Tas-LBA-1	TGTATAATGCTTCTATCGGCAGTACATAGTACATTCCACTGCATATTCGTACATGGCACATAGAGTCAAATCCATTCTTGCCAACATGCGTATCCGGTCCATTAGATCACGAGCTTATTGACCATGCCGCGTGAAACCAGCAACCCGCTTGGCAGGGATCCCTCTTCTCGCTCCGGGCCCATTAACCGTGGGG
Tas-LBA-2	TGTATAATGCTTCTATCGGCAGTACATAGTACATTTTACTGCATATTCGTACATGGCACATAGAGTCAAATCCATTCTTGCCAGCATGCGTATCCCGTCCACTAGATCACGAGCTTGTTGACCATGCCGCGTGAAACCAGCAACCCGCTTTGGCAGGGATCCCTCTTCTCGCTCCGGGCCCATTAACCCGTGGGG
Tas-LBA-3	TGTACAATACTTCCACCGACAGTACATAGTACATTTTACTGTATATTCGTACATATCGTACATAGCACATAAAGTCAAATCCGTTCTTGTCAGCATGCGTACCACGACCCACTAGATCACGAGCTTGTTGACCATGCCGCGCGGAACCCAGCACCCGCTTGGCAAGGATCCCTCTTCTCGCTCCGGGCCCATTGACCGTGGGG
Tas-LBA-4	TGTATAATGCTTCTATCGGCAGTACATAGTACATTATCCGCACATATTCGTACATAGCACATAGCACATAGAGTCAAATCCATTCCTGCAACATGCGTACACATGCACATATATAT
Uch-LBA-1	TGTACAATATCCCTATCGATAGTACATGGCACATTTTATTGTATACCCGTACATAGCGCATGAAGTCAAATCCGTCCACCATGCACATGCCATCACATGCCATCACGAGCTTGTTCACCATGCCGCGTGAAACCAGCAACCCGCTTGGAAGCGAGGATCCCTCTTCTCGCCTCGGGCCCATTAATTGTGGGG

Table S8: Cytochrome b sequences recovered from ancient sheep and goat remains.

Gen_ID KG170112 KG170113 KG170114 KG170118 KG160128 KG170129	Cyth (62 primers) GAGACGTAAACTATGGCTGAATTATCCGATATATACACGCAAACGGGGCATCAATATTTTTTATCTGCCTATTTATGCATGTAGGACGAGGCCTATATTATGGATCATAT GAGACGTAAACTATGGCTGAATTATCCGATATATACACGCAAACGGGGCATCAATATTTTTATCTGCCTATTTATGCATGTGAGACGAGGCCTATATTATGGATCATAT GAGACGTAAACTATGGCTGAATTATCCGATATATCACACGCAAACGGGGCATCAATATTTTTTATCTGCCTATTTATGCATGTAGGACGAGGCCTATACTATCGAGACGAACTATACGAATAACTATGGCTGAATTATCGGATTATATCGAGTCATAC GAGACGTAAACTATGGCTGAATTATCCGATATATACACGCAAACGGGGCATCAATATTTTTTATCTGCCTATTTATGCATGTAGACGAGGCCTATATATA
KG170130 KG170137	GAGATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTTATACATATCGGACCAAGGTCTATATTATGGATCATAT GAGACGTAAACTATGGCTGAATTATCCGATATATACACGCAAAACGGGGCATCAATATTTTTTATCTGCCTATTTATGCATGAGACCAAGGCCTATATTATGGATCATAT
KG170137 KG170139	GAGACGTAAACTATGGCTGAATTATCCGATATATACACGCAAACGGGGCATCAATATTTTTATCTGCCTATTTATGCATGTAGGACGAGGCCTATTATATGGATCATAT
WITH HVRI Gen ID	Cytb (G2 primers)
KG170116	GAGATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA
KG170117	GAGATGTAAATTATGGCTGAATTATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA
KG170120	GAGATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA
KG170121 KG170122	GAGATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGGCATCAATATTCTTTTATCTGCCTATTCATACATA
KG170122 KG160125	GAGATGTAAATTATGGCTGAATCATCCGATACATCACCGCAACCGAGCCTCAATTCTTTATTCTTCCTATTCATACATA
KG160126	GAGATGTAAATTATGGCTGAATCATCCGATACATCACGCCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA
KG160127	GACATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA
KG160129	GAGATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA
KG160130	GAGATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA
KG160131	GAGATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA
KG160132	GAGATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA
KG160133	GAGATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA
KG160134	GAGATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA
KG160135 KG160136	GAGATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGGCATCAATATTCTTTATCTGGCCTATTCATACATA
KG160136 KG160137	GAGATGTAAATTATGGCTGAATCATCCCATACATACATCCGCAAATGGAGCATCAATATTCTTTATCTGCTATTCATACATA
KG170127	GAGACGTAAACTATGGCTGAATTATCCGATATATACACGCAAACGGGGCATCAATATTTTTATCTGCCTATATTATGACGACGAGGCCTATATTACGGATCATAT
KG170127	GAGATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA
KG170131	GAGATGTAAATTATGGCTGAATTATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA
KG170136	GAGATGTAAATTATGGCTGAATCATCCGATACATACACGCAAACGGAGCATCAATATTCTTTATCTGCCTATTCATACATA

Concluding Remarks

The papers in this dissertation focus on applying methods of stable isotope analysis and ancient DNA in order to reconstruct Central Asian pastoralist social connectivity and engagements with the environment over the vast grasslands of Eurasia from the Bronze Age to medieval period. While each paper is a stand-alone study, common themes emerge from their conclusions that shed new light on social processes that have remained elusive in the archaeology of Central Asia. One of the most important themes that is central to this body of research is the multi-scalar prominence of pastoralist subsistence flexibility. This theme is most relevant to Papers 1-3, but it is also implicitly interwoven into Paper 4.

For the study of the medieval period in Central Asia, the Silk Roads remain a key subject of analysis for archaeologists and historians alike. However, the research in Paper 1 provides a new perspective on how the livelihoods of people that drove the commerce of this great exchange network were structured around food. Based on high dietary diversity in "nomadic" communities as revealed through isotopic niche modelling, it is clear that mobile lifeways were marked by a multitude of diverse subsistence strategies compared to people living in urban centers. Traditional studies of the Silk Roads tend to focus on high-value objects being moved long distances as a means to infer social connectivity. This approach fails to consider the everyday interactions of people and the diversity of cultural expressions engrained in communities. Paper 1 takes a different tack by demonstrating how multiresource pastoralism allowed mobile communities to plug into numerous food procurement channels, whereas their urban counterparts shared more monotonous diets that were likely expressive of particular regional cultures. This implies that pastoralists were influential agents of agricultural and food knowledge, given their high degree of inter-individual variety in dietary repertoires. This research provides a means to greatly expand the reconstruction of subsistence practices along the ancient Silk Roads in order to not only further test the unique isotopic patterns observed here, but more importantly to elucidate meaningful human experiences that are often left out of Silk Road history.

While analysis of human remains will continue to be an important aspect of Central Asian archaeology, examining the stable isotopic composition of animals, both domesticated and wild, has great potential in untangling particularities of subsistence strategies in high-resolution. This is especially the case with incremental sampling of herbivore tooth enamel to isolate seasonal patterns in dietary intake that are associated with particular mobility patterns (e.g., vertical transhumance) and manipulation of animal diets with agricultural by-product. The conceptual framework for resolving vertical transhumance in Paper 2 provides a means to assess the frequency that ancient pastoralists accessed high-elevation pastures and to further resolve the year-to-year choices pastoralists made as a reflection of subsistence flexibility.

These fine-grained isotopic records were successfully used to uncover the earliest evidence for agriculture in Inner Asia by isolating winter foddering practices with cultivated millet that had been a new arrival to the steppe zone after its domestication in northern China in the early Holocene. Since human remains from this critical time period are rare, while the actual seeds of domesticated crops are also few, isotopic patterns in livestock provide a novel means to identify agricultural transitions. This approach is one of the most unique cases of scaling up individual life histories at intra-annual scales to reveal the macro process of millet agriculture spreading to the steppe zone during the early third millennium BC. The transmission of millet agriculture has remained mysterious, but with this research, we see that the intensity of cultivation was high at the earliest time of detection and that the knowledge to farm millet was likely a simple retooling of pre-existing know-how for growing wheat and barely. This implies that the spread of pastoralism and plant cultivation

with Near Eastern domesticates to the steppe zone went hand in hand. This research demonstrates that cereal crops are likely to be transmitted faster when accompanying livestock, reflecting powerful combinations of plant cultivation and animal management. Furthermore, this is yet another critical example of multi-resource pastoralism at a time when the first pastoralists were moving into Inner Asia. A synergy between farming and herding provided the capability for pastoralists to carefully adapt subsistence strategies to dynamic social and environmental conditions at the leading edge of this crucial agricultural transmission.

Finally, analysis of ancient DNA from Central Asian goats further corroborated the Inner Asian Mountain Corridor as a key locus of social interaction through which people. domesticates, and ideas flowed for millennia. High mitochondrial genetic diversity present in the foothill zones from the Bronze Age (ca. 1700-1000 cal BC) to Iron Age (ca. 500-100 cal BC) compared to the open steppe landscape strongly suggests that mountains were critical conduits of exchange, rather than barriers to the movement of people and animals. Indeed, this finding echoes the fact that the Inner Asian Mountain Corridor continues to produce the earliest evidence for transcontinental exchanges of cereal crops. Using livestock genetics to infer social connectivity is a novel application of ancient DNA, and future work will help clarify the possibilities and limits of this approach. This ancient DNA study also revealed shortcomings in zooarchaeological classification criteria for Siberian ibex. Specimens that were previously identified as Siberian ibex turned out to be domesticated sheep, as revealed by their cytochrome b genetic sequences. Thus, the importance of hunting by ancient steppe pastoralists may have been less than previously thought, which suggests that more time and energy were spent on synergistic herding and farming to provide subsistence. Hunting may have been an activity to secure prestige if it were practiced infrequently.

While the archaeology of Central Asia continues to be characterized by sparse geographic coverage, this dissertation provides results that fundamentally change our knowledge of how pastoralists in the late Holocene facilitated significant cultural phenomena and influenced settled communities across Eurasia, reflecting an immense spatial and temporal distinction of societies focused on human-animal relationships.

CURRICULUM VITAE TAYLOR RANDOLPH HERMES

trhermes@gshdl.uni-kiel.de

Institute for Pre- and Proto-Historic Archaeology Kiel University 2-6 Johanna-Mestorf-Str. 24018, Kiel Germany +49 176 27555033

Nationality: American

Born: 5 November 1984 in Van Nuys, California, USA

Hometown: Oak Park, California, USA

EDUCATION

Ph.D. (thesis submitted April 2018) Kiel University

The Pastoralist Distinction of Central Asia: Isotopic and Genetic Approaches to Foodways, Mobility and Trans-Regional Interaction from the Early Bronze Age to Medieval Meriod

M.A. (2011) Anthropology, The University of Arizona

Thesis: Pastoral Networks and the Ecological Potential for Understanding Interactions Between Western China and the Eurasian Steppe during the Second Millennium BCE

B.A. (2007) Anthropology, Washington University in St. Louis

Thesis: Ancient Strontium Isotopes and Dynamic Social Interactions of Eastern Kazakhstan

PUBLICATIONS

- Hermes, T.R., M.D. Frachetti, E.A. Bullion, F. Maksudov, S. Mustafokulov, C.A. Makarewicz (2018) "Urban and nomadic niches reveal dietary connectivities along Central Asia's Silk Roads." *Scientific Reports*, 8, 5177
- Hermes, T., Pederzani, S., and C. Makarewicz (2018) "Ahead of the Curve? Implications for isolating vertical transhumance in seasonal montane environments using sequential oxygen isotope analyses of tooth enamel." In *Isotopic Approaches to Pastoralism in Prehistory*, edited by A. Ventresca-Miller and C. Makarawicz. Routledge.
- Hermes, T. and W.A. Longacre (2015) "Rice farming and pottery production among the Kalinga: new ethnoarchaeological data from the Philippines." *Journal of Anthropological Archaeology*, 38, 35-45.

RESEARCH ACTIVITY

2011-Present Co-Director with Drs. Micheal Frachetti and Paula Dupuy

Dzhungar Mountain Archaeological Project (DMAP)

Kazakhstan

Director of stable isotope analysis and zooarchaeology Qarakhanid Archaeology Project Uzbekistan 2015-Present

GRANTS AND RESEARCH DEVELOPMENT

2014 – Present	Doctoral Research Fellowship – Kiel University
2012	Fulbright Grant (Kazakhstan) – United States Department of State
2010	Carrol Kramer Ethnoarchaeology Scholarship – University of Arizona
2010	Je Tsongkhapa Research Grant for Central and Inner Asian Archaeology – University of Arizona
2010	Fred A. Riecker Research Grant – School of Anthropology, University of
2010	Emil Haury Scholarship – School of Anthropology, University of Arizona
2006	Hoopes Undergraduate Research Grant – Washington University in St. Louis

CONFERENCES AND SYMPOSIA

2017	"Substantial Intensity of Millet Agriculture is Revealed in Carbon and Oxygen Isotopic Time Series in Livestock Teeth from Ancient Kazakhstan" – Society for American Archaeology Annual Conference, Vancouver.
2016	"Using δ^{13} C and δ^{18} O Time Series from Livestock Teeth to Reveal the Seasonality of Mobility, Foddering, and Stress during the Bronze and Iron Ages in Eastern Kazakhstan" – International Symposium on Biomolecular Archaeology, Oxford.
2016	"Stable Oxygen and Carbon Isotopic Time-series used to Detect Vertical Transhumance and Foddering in Bronze Age Kazakhstan" – Society for American Archaeology Annual Conference, Orlando, FL.
2014	"Our Complexity Against Theirs: Neolithic Culture in the Altai" – Society for American Archaeology Annual Conference, Austin, TX
2012	"The Neolithic in the Altai Mountains: questioning the uniform rise of pastoralism within a mosaic of hunter-gatherer variability" – Eurasia Archaeology Conference, Cornell University
2011	"Kalinga Rice Farming and Pottery Production" – Society for American Archaeology Annual Conference, Sacramento, CA

2008	"Localized Interaction and Mobile Pastoralism: A Strontium Isotope Approach to the Cultural Geography of Eastern Kazakhstan during the Bronze and Iron Ages" – Oxford University, Challenging Frontiers: Mobility Transition and Change Conference
2006	"Looking at Atoms from the Past and Other Archaeological Finds from Kazakhstan" – Washington University in St. Louis, Department of Anthropology, Archaeology Colloquium
2006	"Bronze Age Steppe Archaeology in Central Asia" Washington University in St. Louis, Undergraduate Research Symposium
AWARDS	
2017	Life Sciences Nord – Kiel University
2011	Excellent in Research Award – School of Anthropology, University of Arizona
2009	Emil Haury Travel Award – School of Anthropology, University of Arizona
2007	Excellence in Research Award – Department of Anthropology, Washington University in St. Louis
2007	Contributions to Anthropology Award – Department of Anthropology, Washington University in St. Louis
2007	First Place Oral Presentation – St. Louis Area Undergraduate Research Symposium
2002-2007	Thomas H. Eliot Academic Scholarship – Washington University in St. Louis
TEACHING EXPE	RIENCE
2016-Present	Instructor for master's level scientific writing and English proficiency – Kiel University
2012	Instructor for undergraduate, upper-level course on ancient civilizations and social complexity
2010-2014	Teaching Assistant for undergraduate archaeology course – University of Arizona
2006-2008	Private tutor for special needs high school students in math and science – Los Angeles and Ventura Counties, California
2005	Advanced English Language Instructor – Babel Summer English Program Shanghai, Hangzhou, and Beijing, People's Republic of China

TECHNICAL AND MEDIA EXPERIENCE

2003-2007 Chief Engineer, Field Talent, and DJ – KWUR 90.3 FM "St. Louis Underground Radio" – St. Louis, Missouri

2002-2006 Television Broadcasting Engineer – Aerial Video Systems – Burbank, California