A new zooarchaeological application for geometric morphometric methods: Distinguishing *Ovis aries* morphotypes to address connectivity and mobility of prehistoric Central Asian pastoralists

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Abstract

Geometric morphometric methods (GMM), which were developed to characterize the shape and size of biological organisms, have been applied within zooarchaeology over the past decade to address animal domestication processes and to refine morphological criteria to differentiate between taxa. However, there has been limited utilization of these methods to discriminate between populations of the same taxa to challenge and refine other key archaeological issues, such as migration and connectivity in prehistory. Presented here is a novel application of a three-dimensional landmark based geometric morphometric approach to address the nature of long distance trade and connectivity on the prehistoric Silk Road. The similarity of Bronze and Iron Age archaeological cultures along this steppe route has encouraged characterisations of these people as nomads, with highly mobile, integrated, and connected human and animal populations. However, the interconnectedness of domestic animal populations, in particular sheep (*Ovis aries),* the foundation of this prehistoric pastoral economy, has never been examined. This study utilized geometric morphometric methods to quantify geometric morphometric variance of *O. aries* astragali between three geographically disparate settlement sites within a single Final Bronze age cultural and chronological context. Significant differences between morphotypes revealed that protracted mobility patterns were unlikely and that while animal exchange may have occurred, it was not pervasive enough to produce a uniform sheep morphotype across central and southeastern Kazakhstan. The result of this new application of geometric morphometric methods challenges models of uniform and undifferentiated long distance mobility and economic connectivity between the peoples of the Silk Road.

KEYWORDS: GEOMETRIC MORPHOMETRICS; ZOOARCHAEOLOGY; PASTORALISM; OVIS ARIES; BRONZE AGE; CENTRAL ASIA; THREE-DIMENSIONAL DIGITISATION

Introduction

Trade, connectivity, and mobility are key components in the study of early globalisation processes. The Central Asian steppe was a key region for the transfer of agricultural goods between Asia and Europe, and is well known as the Silk Road in the historical period, which was underpinned by trade, widescale mobility and migration (Jones et al., 2011; Miller et al., 2016; Spengler et al., 2016). Yet the degree and role of mobility in the formation of social networks and cultural change is still poorly described. Demic models of cultural change have recently found new support with the publication of human genetic data indicating mass migrations both from and within the Central Asian steppe in the Early Bronze Age (Allentoft et al., 2015; Chernykh et al., 2008; Damgaard et al., 2018b, 2018a; Frachetti, 2011; Haak et al., 2015; Kuzmina, 2008; Narasimhan et al., 2018). However, cultural diffusion models are still preferred to describe the gradual cultural changes of the Late and Final Bronze Age in Central Asia prior to the increasing social inequality and technological advances associated with the Early Iron Age. These pastoral economies, with little evidence of agricultural production, are based upon animals, and as these animals are mobile assets, it has long been assumed that mobility was a key feature of both human and animal populations. The scale of interaction between human settlements through this period is disputed, with models of long distance mobility over thousands of kilometres influenced by ethnographic examples and widespread material cultures (Kuzmina, 2007). These compete with localised network models that emphasize limited pastoral circuits, such as vertical transhumance and tethered mobility, that link together to form broad networks of material culture exchange (Bendrey et al., 2010; Frachetti, 2009; Rouse and Cerasetti, 2018). Recent archaeological research has supported the latter, with increasing evidence for localised lifeways and economies that share an overarching material culture (Haruda, 2018; Motuzaite Matuzeviciute et al., 2015; Spengler et al., 2013; Ventresca Miller et al., 2017). While traditional zooarchaeological analysis has contributed to this debate, morphological variability of animal bones has not yet been explored. Osteological remains contain ecomorphological variation that vary by population, and especially for postcranial elements can signal local ecological adaptation. Geometric morphometrics capture and measure this variation, which makes this method ideal for directly addressing archaeological questions of connectivity and exchange.

As a small, mobile herd animal, sheep are ubiquitous across prehistoric steppe archaeological contexts dating from the Early Bronze Age as part of a pastoral package of horse, cattle, and goats, (Bendrey, 2011; Haruda, 2018; Outram et al., 2012). Zooarchaeological assemblages are analysed as palimpsests, with animal remains from the same chronological context within a site analysed as one unit to assess economic patterns at a particular settlement for that period (Reitz and Wing, 1999). It is unclear if Central Asian sheep flocks were part of a single highly intermixed flock, in the same manner as predominant material culture groups. Ethnographically in the nineteenth and twentieth centuries, livestock were exchanged between pastoral families and to secure social contracts (Abramzon, 1971; Gardner and Shayakhmetov, 2006; Hudson, 1938; Krader, 1955; Olcott, 1987). These types of exchanges led to the development of a Central Asian fat-tailed sheep landrace that was found throughout the region during this historical period, but has since been lost due to admixture with European breeds in the past century. (Mason and Porter, 2002; Olcott, 1987; Robinson and Milner-Gulland, 2003; Youatt, 1837). Animal exchange in prehistory would have also resulted in regionally similar flocks that were not isolated and continually subject to admixture. Uniform long-distance mobility patterns practised by pastoralists across the region would have encouraged similar osteological morphotypes adapted for extensive seasonal migrations that overrode the influence of local ecology (Kuzmina, 2007). Both social contracts secured by animal exchange and long distance mobility would lead to a homogeneous sheep flock across the Central Asian steppe, which can be tested via geometric morphometric methods.

The power of geometric morphometric methods lies in the ability to detect small but significant changes in shape between groups of specimens whilst retaining the element of shape information related to size. These significant differences are often lost in traditional quantitative and qualitative measurement methods (Zelditch et al., 2012). Zooarchaeologists have used size differences to examine the effects of domestication and cultural change, but have only been able to roughly describe shape quantitatively using ratios of linear measurements or logarithm methods (Albarella, 2002, 1997a; Sykes et al., 2013; Thomas, 2005; Zeder et al., 2006). While linear measurements of appendicular skeletal elements are useful in zooarchaeology for species delineation and in certain archaeological contexts, such as the size change of a species through time (Albarella, 1997b; Davis, 2000; Rowley-Conwy, 1998; Sykes et al., 2013), the confounding factor of size upon these elements can cloud attempts to distinguish between populations and early emerging landraces. Guidelines developed in the middle of the last century for identifying sheep breed types, such as the ‘fat-tailed’ sheep typical of the steppe, utilize withers heights which are calculated using greatest lengths of appendicular limb bones (Tsalkin, 1961). These measurements are affected by ontogenetic variables, which are biological variables that impact bone morphology such as sex and nutritional level, and have since been found to be unreliable for discriminating between breeds of sheep (Popkin et al., 2012).

Geometric morphometrics have been used to explore domestication and population variation, with specific focus upon the morphology of skulls and teeth (Bopp-Ito et al., 2018; Drake et al., 2015; Duval et al., 2018; Owen et al., 2014). Other skeletal elements which are more resistant to density-mediated attrition, such as calcanei, have been used successfully in ecomophological and archaeological investigations of variability between populations (Barr, 2014; Bignon et al., 2005; Curran, 2012; Plummer et al., 2015, 2008; Pöllath et al., 2019). Measurement of morphological variation of zooarchaeological remains requires careful selection of a skeletal element that is both taphonomically robust as well as appropriate for measuring inherited traits that address the archaeological research question.

The astragalus has the least amount of growth out of all appendicular elements in the *O. aries* skeleton and only occurs via appositional growth across the medio-lateral axis (Popkin et al., 2012). Nutritional level, sexual dimorphism, and remodelling affect the astragalus the least out of all post-cranial elements as it is completely enclosed within the joint and does not have a secondary ossification centre (Pöllath et al., 2019). This element is a key bone in the ankle joint of the animal, and works as a pivot point to convert motion both distally and dorsally. Working in concert with the calcaneus, the astragalus controls for the degree of flexibility and stability in this joint. The morphology of the distal articulation and the shape of the plantar articular surface together form a disc cam, improving efficiency of stride for cursors (Barr, 2014). The astragalus has been noted as effective as an ecomorphological indicator in studies of bovid post-cranial elements to reveal the ecological and topographical environment of ancient animals (Curran, 2015; DeGusta and Vrba, 2005; Plummer et al., 2008; Pöllath et al., 2019). The environment of a ruminant flock, even within the same species, drives selection towards a more efficient ankle joint for movement through the closed or open environments, with populations living in closed environments with extensive vegetative cover or mountainous gradients possessing ankle joints which are optimized for mobility and powerful movement. Populations in open environments, such as the steppe or savanna, have ankle joints optimized for speed and stability (Curran, 2012; Plummer et al., 2008). The astragalus is a robust element that survives well taphonomically and is resistant to density-mediated attrition and as this element the least affected by ontogenetic variables, the astragalus is an excellent specimen for measuring inherited osteological morphology that reflects site palaeoecology (Lyman, 1994). Shape variation between individuals is to be expected, however overall morphology of the astragalus across a population of *O. aries* represents an ecomorphotype for that particular population.

As osteological remains contain ecomorphological variation that is influenced by human-mediated mobility patterns and dispersals across the ancient landscape, morphotypes particular to a locality would indicate that inherited morphotypes are specific for that palaeoecology, while a general morphotype that is uniform across sites and regions would indicate interbreeding between regional flocks or a high degree of long-distance mobility to negate the effect of a specific environmental influence around site environs. As zooarchaeological collections are palimpsests that represent the animals which were deposited during the period of occupation of the site, these remains represent a sample of animals during the occupation periods. Here, specimens from each site are referred to as a population, which refers to a geographically distinguished group of animals that occurred as a zooarchaeological palimpsest during a period of interest (Pöllath et al., 2019). Thus, this novel study evaluates osteological morphology between Final Bronze Age *Ovis aries* populations to test whether flock homogeneity aligns with material cultural homogeneity as a proxy for describing the degree of connection between human settlements.

Materials and Methods

Ovis aries astragali were selected from zooarchaeological assemblages from three Final Bronze Age settlement sites in central and southeastern Kazakhstan, a region encompassing roughly 450,000 km^2. These specimens are from the publicly held archaeological collections of E.A. Bukhetov Karaganda State University, Karaganda and the Margulan Institute for Archaeology, Almaty. No permits were required for the described study. Neonatal specimens and those with surface damage that would affect landmark placement were excluded from the study. Both left and right specimens were selected except in cases in which entire articulated skeletons were excavated within a single context, in which case the left astragalus was selected. Astragali were identified to species according to qualitative characteristics (Boessneck, 1969; Fernandez, 2001; Prummel and Frisch, 1986; Zeder and Lapham, 2010) and this was tested using geometric morphometric methods (Haruda, 2017).

The Final Bronze Age sites of Kent, Serektas, and Turgen, are located in different agro-climatic zones with varying degrees of topographic variation (Haruda, 2018) (Fig 1). Kent is a large archaeological settlement with one hundred and thirty pit houses and located at 925 m a.s.l. in the central Kazakh highlands within Karkaralinsk National Park. This area is characterized by granitic outcrops which rise to 1350 m a.s.l. within the park boundary and have a higher biodiversity than the surrounding steppe. It is forested with pine and birch while the surrounding semi-arid steppe is largely comprised of dry fescue type grasses and *Artemisia* spp. Kent is dated by ceramic typology to the Final Bronze Age (1300-900 BCE) and belongs to the Begazy-Dandybaevsky material culture group (Epimakov et al., 2005; Evdokimov and Varfolomeev, 2002). Previous zooarchaeological analysis has shown that this settlement was heavily reliant upon sheep and goat which formed 63% of recovered identifiable remains (NISP) and were likely raised for meat with a majority of the population slaughtered before reaching four years of age (Haruda, 2018; Outram et al., 2012). Eight astragali from *Ovis aries* originate from this site and are housed at the Bukhetov Karaganda State University in Karaganda, Kazakhstan (SI Table 1).

Fig 1. Location of archaeological sites

Serektas is located at 776 m a.s.l. in the semi-arid steppe located midway between the Tien Shan mountains 100 km to the south and the shores of Lake Balkhash 150 km to the north. The site is a small settlement comprised of a pit house with multiple phases of renovation and occupation. Serektas is also dated to the Late and Final Bronze Age by the presence of Begazy-Dandybaevsky ceramics (Yermolaeva, 2001, 2000). The zooarchaeological profile of this site is similar to Kent, with ovicaprids comprising 48% of NISP, although over half of the population survived past four years of age (Haruda, 2018). Ten *Ovis aries* astragali originate from this site and are housed at the Margulan Institute of Archaeology in Almaty, Kazakhstan.

Turgen is located at 1900 m a.s.l in a lightly wooded conifer valley within the foothills of the Tien Shan mountain range. The Turgen valley originates at the foot of a glacier at approximately 3500 m a.s.l and emerges onto the Semirech'ye alluvial plain near the modern city of Talgar at 1000 m a.s.l. The site, located midway up the ravine, is comprised of two pit houses and two nearby cemeteries. and also is dated by the presence of Begazy-Dandybaevsky ceramics from Late and Final Bronze Age (Goriachev, 2011a, 2011b; Roberts et al., 2019). Despite the difference in microclimate and rainfall, the zooarchaeological signature at Turgen is very similar to the other two site, as 53% of NISP are ovicaprid, with a strong indication for meat consumption, with less than 10% of the population surviving past four years (Haruda, 2018). Twenty-one *Ovis aries* astragali from this site contributed to this study and are also housed at the Margulan Institute of Archaeology in Almaty, Kazakhstan.

Digitising and Landmarking

A suite of fifteen landmarks selected for this analysis follow a previously published set of landmarks (Haruda, 2017) and describe the shape of the *O. aries* astragalus following quantitative and qualitative zooarchaeological literature (Boessneck, 1969; Fernandez, 2001; Prummel and

Frisch, 1986; von den Driesch, 1976; Zeder and Lapham, 2010) as well as literature which describes landmark methods for the appendicular morphology of *Cervidae* (Curran, 2015, 2012; Sykes et al., 2013) (Fig 2). Specimens were scanned using a Next Engine 3D Laser Scanner with a dimensional accuracy of ± .381 mm at a resolution of 2500dpi with Scan Studio HD software. These scans were aligned to at least an accuracy of ±0.02mm and fused together into a single three-dimensional mesh. Once scans were trimmed, aligned and fused, they were imported as cloud data (.ply) into Landmark Editor (Wiley et al., n.d.). Landmarks were located on each specimen visually and with the assistance of plantar-dorsal and proximal-distal axes according to landmark criteria and these files are deposited in an open-access data repository (Haruda, 2017)(10.5281/zenodo.1188830).

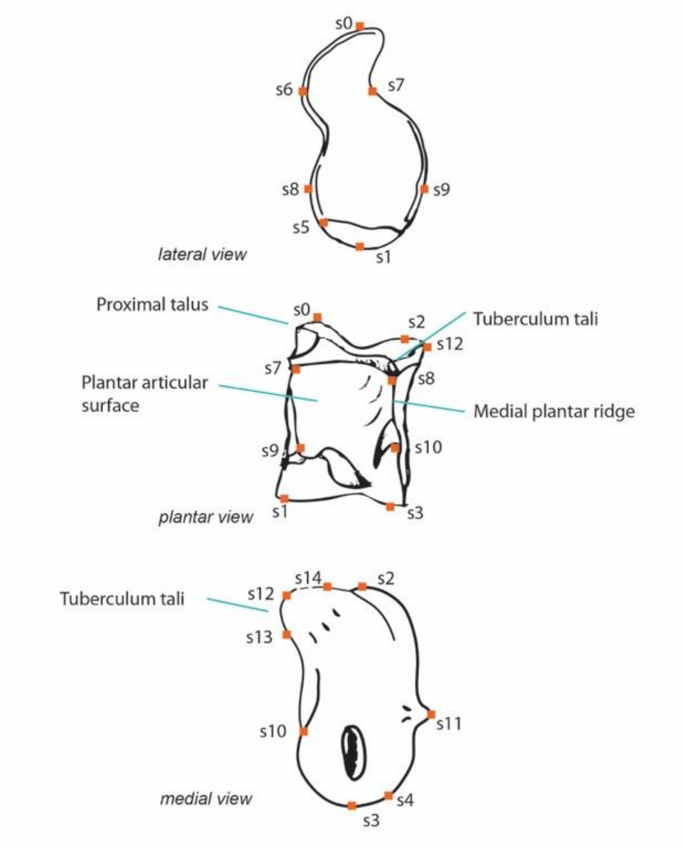

Fig 2: Landmark locations

Statistical Testing

The data were superimposed using a Generalized Procrustes Analysis (GPA) in MorphoJ to scale all configurations to centroid size, translate them to the same location, and rotate them to the same orientation and reflect them so both left and right specimens were comparable (Dryden and Marida, 1998; Klingenberg, 2011; Rohlf and Slice, 1990).

Measurement and replication error was quantified with a Procrustes ANOVA in MorphoJ on a larger set of data from Serektas that incorporated two additional *Capra hircus* models which was previously published (n = 12) (Haruda, 2017; Klingenberg, 2011; Klingenberg and McIntyre, 1998). Specimens were scanned twice to create three-dimensional models, and each model was landmarked twice, resulting in four sets of landmarks for each specimen. It was found that variation between specimens was greater than between replicates, indicating that measurement error was negligible (SI Table 2).

Statistical testing to investigate the influence of size and allometry as well as to explore variation within the data was conducted using the packages Morpho and Geomorph in R (Adams et al., 2017; Adams and Otárola-Castillo, 2013; R Core Team, 2017; Schlager, 2017). Significance of size variation was tested with a Kruskal-Wallis test using log centroid size by site, and found a p value of 0.11 which was not significant for variation between sites. The presence of allometry was tested using a multivariate regression of shape (Procrustes coordinates) upon size (log centroid size) with 1000 permutations and a randomised residual permutation procedure (RRPP) and allometry was not found to be significant and size did not affect shape. To test for the effect of allometry across sites, a single factor MANCOVA, with Procrustes coordinates as dependent, log centroid size as independent, and sites as a factor with 1000 permutations and a RRPP also found that allometry was not significant. Furthermore, a homogeneity of slopes test found that slopes of sites were parallel and that allometry was not a significant effect between sites.

Due to the small sample size, large number of variables in comparison to specimens, and the known problems with over fitting of classification rates with this type of data, the dimensionality of the data was reduced using a Principal Components Analysis (PCA) in which components that accounted for over 95% of variation were subsampled for a canonical variate analysis (CVA). The CVA, paired with a leave-one-out cross validation, was used to test for differences in shape between groups (Klingenberg and Montero, 2005; Viscosi and Cardini, 2011; Zelditch et al., 2012). To visualize the variations between groups, a between-group PCA was utilized as this method does not overestimate the extent of separation between groups. The mean shapes of groups and visualizations of morphological variation were conducted by morphing the variation associated with each principal component at a magnification of three standard deviations onto a three dimensional model of the grand mean shape of all the specimens using the morphing functions of Geomorph (Adams et al., 2017; Adams and Otárola-Castillo, 2013) (Fig 3). This method was also used to test group membership using a permutation test of difference of average shape for pairwise comparisons (Table 2).

Results and Discussion

Permutation tests of the difference of average shape were significant (Table 1) across all pairwise comparisons. The smallest Procrustes distance between groups was between Serektas and Turgen. This is reflected in the cross-validated classification rates for the between-group PCA in which Serektas and Turgen have a lower correct classification rate than Kent (Table 2). Cross-validated classification rates for a canonical variate analysis with a reduced dimensionality return a 100% correct classification rate, indicating that there is slight overfitting using this type of analysis, even with a reduction in dimensionality.

Table 1. Pairwise Procrustes distances among site (above the diagonal) and p-values for the null hypothesis of equal means (below the diagonal).

	Kent	Serektas	Turgen
Kent	-	0.08800339	0.06858336
Serektas	0.0001	-	0.05934617
Turgen	0.0001	0.0001	-

The first between-group principal component accounted for more than half of the shape variation in the dataset [62.6%] while the second principal component accounted for a third of the shape variation [37.3%]. Specimens from each of the three sites clearly clustered apart along both the first and second principal components (Fig 3). Predicted shape variation along the first principal component revealed variation in the orientation of the tuberculum tali, which lies medially to the plantar articular surface that meets the calcaneus (Fig 2). The tuberculum tali was oriented laterally towards the plantar articular surface for specimens with a positive value on the first principal component, while it was oriented medially for those with negative values. Additionally, astragali with positive values of the first principal component were elongated. Morphological variation along the second principal component revealed a greater difference between the maxima of the proximal and distal trochlea.

Table 2. Cross-validated classification results in percentages, with sample size in brackets

	bgPCA			**CVA**			
	Kent	Serektas	Turgen	Kent	Serektas	Turgen	None
Kent	100% (8)	0 %(0)	0% (0)	100% (8)	0% (0)	0% (0)	0% (0)
Serektas	0% (0)	90% (9)	10% (1)	0% (0)	80% (8)	0% (0)	20% (2)
Turgen	0% (0)	14.28% (3)	85.71% (18)	0% (0)	0% (0)	100% (21)	0% (0)
Overall classification accuracy: 89.7%				Overall classification accuracy: 94.9%			

This landmark-based geometric morphometric method was able to reveal statistically significant differences in morphology between astragali from three different archaeological sites. The visualisation of shape variation along the first and second between groups principal components indicated differences in the functionality of the ankle joint. The tuberculum tali, located on the proximal medial corner of the plantar articular surface marks the full extent and angle of articulation with the distal tibia. As the sustentaculum tali of the calcaneus slides along the plantar surface of the astragalus, it follows the prominence of the plantar ridge. Any reduction in the prominence of features such as this plantar ridge would result in a less stable and more mobile joint (Barr, 2014; Plummer et al., 2015, 2008). The degree of mobility is marked by the relative size of the trochlea, while stride length is marked by the location of a divot on the distal half of the plantar surface. The relative increase in articular surface area on the plantar aspect increased stride length and efficiency of movement but decreased power for intense bursts of motion. Conversely, squatter astragali with robust trochlea with shorter plantar articular surfaces increased stride power and mobility with fewer prominent features were characteristic of closed environments.

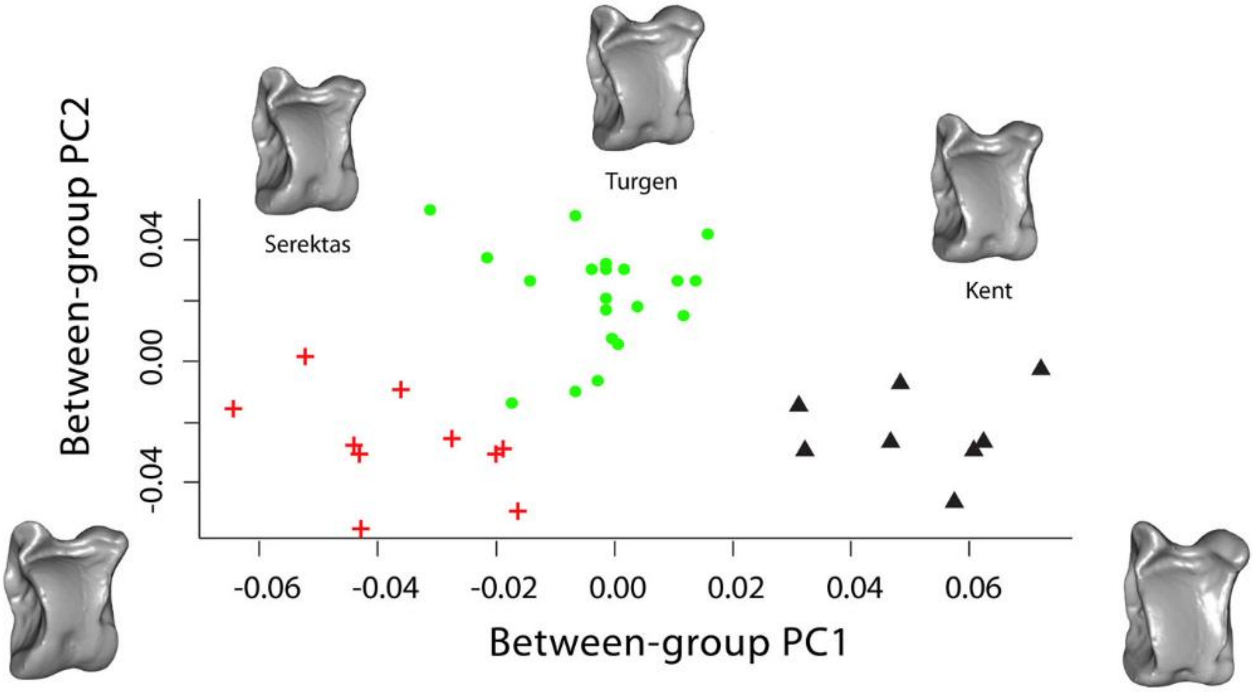

Fig 3. Between-group principal component analysis and average site shapes. Scatterplot of the scores along the first two between-group principal components. Overlaid are predicted shape changes along the first between-group principal component with a magnification factor of three and the average shape of astragali from each site.

Astragali from Serektas are relatively gracile and have morphological features including a less prominent tuberculum tali and proximal tali with a shallow groove. These astragali also have a shorter plantar articular surface and a prominent divot on the distal end of this surface, indicating a wider range of flexion on the distal end of the joint. The specimens from Turgen have a similar morphology to those from Serektas, with a less prominent tuberculum tali and a shorter plantar articular surface, however with even less prominent trochlea which would encourage even more joint mobility. In contrast, specimens from Kent are squat and robust and have a longer plantar articular surface, a more prominent tuberculum tali and plantar articular ridge as well as a more compact distal end, better for more efficient movement through open environments.

Specimens from Kent clearly possess morphological traits associated with open environments. In contrast, specimens from Turgen and Serektas have a more closed morphology, although these are not consistent for these two sites. The forested and vertiginous environment of Turgen is very different from the flatter topography surrounding Kent and Serektas. It is likely that specimens at Serektas had access to the foothills of the Tien Shan, as this site located only eighty kilometres from these mountains and thus individuals may have been grazed in both open and closed environments. Furthermore, the cross-validated classification results also indicate that there may have been some connection between populations or exploitation of similar types of topography for some individuals at Serektas and Turgen.

As established above, astragalus morphology is not affected by ontogenetic variables and is the closest to a phenotypic expression of inherited traits, rather than reflecting plasticity driven by variation in pasturage, proportions of sex hormones, or changes to morphology due to remodelling. Recent GMM research on astragalar morphology has shown that variation in the width of the distal end (the Bd measure in traditional von den Driesch 1976 linear measures) does vary by age, but not by sex or environment (Pöllath et al., 2019). The morphotypes here show a range of variation across the entire specimen, but variation at the distal end is not the most prominent area of variation. Furthermore, previous herd profiles of sheep at these three sites show similar slaughter patterns, with few animals surviving past three years of age. As astragali were selected once fully ossified, which occurs at eighteen months of age, we can assume that this age range for this sample is relatively narrow and that the variation between site morphotypes is not due to age related slaughtering patterns.

The ankle joint is key to movement efficiency and thus survival. Animals which were unable to efficiently move long distances to access distant pastures or move through closed environments and evade predators were more likely not to pass on their genes to the next generation. Therefore, the morphological signature of the astragalus is associated with the amount of cover and topography of each site, which confirms the specificity of each population to a respective microenvironment and can be called an ecomorphotype. This ecomorphological specificity indicates that mobility of these sheep populations was limited to the local environment of the human settlement, and for example, sheep at Turgen were not participating in long distance migrations across the relatively flat steppe, nor were sheep at Kent utilizing vertiginous areas for pasture.

The clear separation of ecomorphotypes of sheep astragali in the Final Bronze Age can be the result of two possibilities- the development of rapid ecomorphological adaptation or genetically distinct sheep populations. These interpretations are not necessarily mutually exclusive. The genetic structure of this ancient sheep population is not yet clear and it still remains to be seen whether ancient sheep were introduced from the same founder population, or were the result of separate introductions in the Early Bronze Age (Anthony, 2007). While the phenotypic link between some elements in some species has been tested, such as for pigs, for this element in sheep, the direct correlation between genetic variation and morphotype is not yet established. Furthermore, the speed at which this ecomorphological adaptation occurred within populations is still not yet well understood and necessitates future research.

Additionally, the quantification of the morphological variation between modern sheep breeds and these ecomorphotypes would further serve to illustrate the relationship between ancient and modern animal populations, particularly to explore whether these prehistoric sheep had similar morphologies to modern sheep breeds, such as the historic fat-tailed Central Asian breed. However, this is secondary to exploring the nature of the sheep flock homogeneity in the Final Bronze Age and would not address questions of connectivity and exchange. Despite the origin of this particular morphological plasticity, the geometric morphometric results point to isolated populations with little animal exchange and separate, local pastoral mobility patterns in the Final Bronze Age within a single shared cultural community that refutes hypotheses of a uniform and interconnected steppe-wide sheep flock as well as long-distance mobility patterns.

These non-homogenous *O. aries* morphotypes support recent models of multi-scalar pastoral exchange and interaction. First proposed as non-uniform interactions across the steppe (Frachetti 2009), the multi-scalar model was developed to describe the nature of sedentary/mobile interaction (Rouse and Cerasetti, 2018) and applies well in this context to describe the nature of intra-cultural exchange and connectivity between the central steppe and the southeastern region of Kazakhstan. While material culture, burial customs, and architectural forms across this large region of central and southeastern Kazakhstan were similar in the Final Bronze Age, variation between sheep morphotypes indicates that local economies and scales of mobility were circumscribed in comparison to the sphere of exchange of ideas, material culture, and modes of life. Zooarchaeological analysis of herd structures of cattle, horses, and ovicaprids from these settlement sites support this, as proportions of cattle in the Semirech'ye during the Late and Final Bronze Ages are more similar to settlements of the same material culture located in more arid regions of the central steppe (Haruda 2018). This is in contrast to broader patterns of domestic animal exploitation across Eurasia during the Bronze Age, in which the proportions of cattle present at settlement sites correlates strongly with annual precipitation and ecoregion (Bendrey, 2011; Outram et al., 2012). Thus pastoralism as an economic mode is shared across this region, while the local practice, at least for the management of sheep flocks, is locally circumscribed with little connectivity and exchange of animals. However, mobility of other domesticated species, particularly those which would facilitate human connectivity, such as horses and camels, is not yet know, and if studied, would further clarify the degree of human interconnectivity during this period. It is clear that there is good evidence for long distance exchange at this period and in the following Iron Age as millet and other crops moved along the prehistoric Silk Road, yet the nature of this dispersal, whether diffusing slowly through neighbouring communities, or via individuals moving long distances on horses is still unclear. However, during this particular chronological context, long distance mobility and connectivity of entire communities and their flocks of sheep can be excluded as a model for trade and connection along the Silk Road.

Conclusion

Landmark based three-dimensional geometric morphometric methods using a post-cranial element, the astragalus, on zooarchaeological remains successfully revealed significant morphological variation between Final Bronze Age sheep located at different settlement sites. The presence of these three distinct morphotypes challenges assumptions of *Ovis aries* flock homogeneity and archaeological models which emphasize long distance mobility as an essential component of pastoralism. This is some of the earliest direct evidence which indicates that connectivity and exchange between settlements within a cultural community was complex and multi-scalar. Comprehensive movements of people with their flocks across immense distances on annual migrations no longer appears to be a likely model for prehistoric pastoral patterns and human networks. Instead, communication and exchange of material culture and ideas occurred at diffuse and varying scales which linked together human settlements across the prehistoric Silk Road.

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