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Subsistence strategies of prehistoric hunter-gatherers on the Tibetan Plateau during the Last Deglaciation

Jian WANG[1], Huan XIA[1], Juanting YAO[1], Xuke SHEN[1], Ting CHENG[1], Qianqian WANG[2] & Dongju ZHANG[1*]

[1] *Key Laboratory of Western China's Environmental Systems (Ministry of Education), College of Earth Environmental Sciences, Lanzhou University, Lanzhou 730000, China;*
[2] *Qinghai Provincial Institute of Cultural Relics and Archaeological Research, Xining 810007, China*

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Abstract The study of prehistoric hunter-gatherer subsistence strategies on the Tibetan Plateau is important for understanding the mechanisms and processes of human adaption to high altitude environments. But to date, only a few Paleolithic sites have been found on the Tibetan Plateau with clear stratigraphy and reliable dating. These sites are mainly distributed in the Qinghai Lake Basin on the northeastern part of the plateau, and the sporadic fauna and flora remains excavated provide limited information about the subsistence strategies of hunter-gatherers. In 2014, relatively abundant animal remains were unearthed in the Lower Cultural Layer (LCL, 15400–13100 cal yr BP) of the "151 site" located in the Qinghai Lake Basin, providing important information about human subsistence strategies on the Tibetan Plateau during the Last Deglaciation. Zooarchaeological analysis of these faunal remains indicates that hunter-gatherers at the "151 site" mainly targeted large ungulates of *Bos* and wild horse/ass, and only brought back the most nutritious parts of animal carcasses including upper and intermediate limb bones, heads, and trunks (ribs and vertebrae). People then processed and consumed the carcasses around single hearths. Our comprehensive analyses of contemporaneous sites in the Qinghai Lake Basin show that a subsistence strategy involving opportunistic hunting of ungulates, high mobility, and short occupation of campsites was used by terminal Pleistocene hunter-gatherers to adapt to the high-altitude environment on the Tibetan Plateau. This subsistence strategy may have been a first step of gradual hunter-gatherer adaptation to the extreme conditions on the Tibetan Plateau after the Last Glacial Maximum, and laid the foundation for the widespread distribution of hunter-gatherers on the plateau during the Holocene.

Keywords Tibetan Plateau, Last Deglacial, 151 site, Hunter-gatherers, Taphonomy, Zooarchaeology, Subsistence strategy

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1. Introduction

The Tibetan Plateau holds a central place in research on prehistoric human-environmental relationships in extreme environments, especially for understanding prehistoric human adaptation to high-altitudes. Since the 1970s, prehistoric human activity and human adaptation to high-altitude environments have attracted the interest of scientists from many disciplines (An et al., 1979; Tang, 1999; Brantingham et al., 2003, 2010; Brantingham and Gao, 2006; Madsen et al., 2006; Yuan et al., 2007; Gao et al., 2008; Yi et al., 2010; Huerta-Sánchez et al., 2014; Chen et al., 2015, 2019; Zhang D J et al., 2016, 2017, 2018; Meyer et al., 2017; Zhang X L et al., 2018). However, due to the lack of Paleolithic sites with secure stratigraphy and reliable dating results, the history of prehistoric hunter-gatherers on the Tibetan Plateau still needs further clarification. Recent studies have successively updated our understanding of prehistoric human history on the

* Corresponding author (email: djzhang@lzu.edu.cn)

plateau. For example, research at the site of Nwya Devu (ND) reveals that Modern Humans occupied the plateau nearly 4600 m above sea level (masl) at least 30–40 thousand years before present (kyr BP) during the Last Glacial (76–11.7 kyr BP) (Zhang X L et al., 2018). In addition, systematic study of the Xiahe mandible (XH) reveals that an ancient group of Denisovans or a Denisovan-related population may have occupied the Tibetan Plateau at least 160 kyr BP during the Penultimate Glacial (190–130 kyr BP). This population provides a possible local source of the EPAS 1 allele (Endothelial PAS domain-containing protein 1), a widely existing high-altitude environmental adaptation gene shared between Denisovans and modern Tibetans (Huerta-Sánchez et al., 2014), and further reveals that a Denisovan-related population may have successfully adapted to the high-altitude environment before Modern Humans (Chen et al., 2019). These two studies not only greatly extend human history on the plateau, but also provide wider space for studies of early human adaptation to high-altitude environments. Nevertheless, without associated fauna and flora remains, neither of these two studies has answered the question about how early human survived behaviorally in this high, cold, hypoxia, and resource-scarce environment.

Access to adequate food resources is essential for human survival. Therefore, the study of food resource utilization strategies is a key to understanding early human adaptation to the plateau environment. Chen et al. (2015) has described agropastoral subsistence strategies on the plateau in the middle and late Holocene, arguing that agriculture and animal husbandry provided reliable food resources for Neolithic-Bronze Age humans to permanently settle on the high altitude Tibetan Plateau. In comparison, hunter-gatherers could only rely on wildlife resources before the emergence of agropastoral economy. At present, Paleolithic sites with known reliable dates on the plateau are mainly distributed in the Qinghai Lake Basin during the Last Deglaciation (18–11.7 kyr BP), and include Jiangxigou 1 (JXG 1), Heimahe 1 (HMH 1), Locality 93-13, 10HTHS 1, HZYC 1 and Bronze Wire Canyon 3 (BWC 3) (Madsen et al., 2006; Yi et al., 2011; Rhode et al., 2014). During the Last Deglacial Period, the climate gradually became warm and wet on the plateau, attracting hunter-gatherers to visit more frequently from neighboring low-altitude regions (Zhang D J et al., 2016). A few faunal remains from the above sites collected during surveys and test excavations have provided some limited information, indicating medium-to-large deer-sized and small-to-medium gazelle-sized mammals had been hunted in Qinghai Lake Basin during the Last Deglacial (Madsen et al., 2006, 2017; Yi et al., 2011), but it is insufficient to thoroughly understand prehistoric hunter-gatherers' subsistence strategies on the Tibetan Plateau. Today, gazelles are the most abundant wild ungulates across the Tibetan Plateau, besides wild yak and wild ass who distributed mainly in regions above 4000 masl.

Here, we present a detailed analysis of faunal remains from the lower cultural layer (LCL) of the "151 site", the first Epipaleolithic site excavated in the Qinghai Lake Basin. Using accelerator mass spectrometry (AMS) ^{14}C dating combined with systematic zooarchaeological and taphonomic analysis, we aim to draw a better picture of prehistoric hunter-gatherers' subsistence strategies on the Tibetan Plateau during the Last Deglacial Period.

2. The study site

The "151 site" (36.560°N, 100.475°E, 3397 masl) is located near the 151 scenic area of Jiangxigou town, Gonghe county, Qinghai province. It is located at the foothill of the north slope of Qinghainanshan Mountain in the southern Qinghai Lake Basin, and to the east of a small river which flows to Qinghai Lake from the south. It is about 3.5 km south of Qinghai Lake and 203 m above the modern lake level (Figure 1a and 1b). The "151 site" was discovered by a Sino-US joint investigation team in 2007 (Yi et al., 2011). In 2014, the Qinghai Provincial Institute of Cultural Relics and Archaeological Research and Lanzhou University conducted excavations at the site, with an excavation area of 25 m^2 (5 m×5 m) and a final excavated depth of about 3.4 m. In addition to the previous known early-middle Holocene cultural layer (Rhode et al., 2014), which we refer to as the Upper Cultural Layer (UCL), a new cultural layer, which we refer to as the Lower Cultural Layer (LCL), was found in the northwest corner of the excavation about 2.8-m below the surface (Figure 1c). There is about 0.8-m-thick natural loess deposits between the UCL and LCL. Here we only analyze the faunal remains from LCL. Archaeological remains from UCL will be discussed in other papers.

LCL was only present about 3 m^2 in the northwest of the excavation and was only about 20 cm thick. It was mainly composed of a single hearth and associated archaeological remains, and no temporary architectural features were found around them (Figure 1d). The hearth was roughly elliptical (90 cm×50 cm) and its structure was simple. A large amount of charcoal, hearth rocks, stone artifacts, and bones were distributed in the hearth and some were scattered outside. Diameters of the hearth stones were mostly between 5 and 12 cm and many of them were cracked, indicating that they had been burned. Not many stone artifacts were found. Stone artifacts were mainly consistent with the small-flake-tool industry of North China, with a few pieces of microblades and very few finished tools. Lithic technology and artifact type composition in the LCL are consistent with contemporaneous JXG 1 and HMH 1 sites in Qinghai Lake Basin (Madsen et al., 2006). Animal bones from LCL were relatively numerous, but very fragmented.

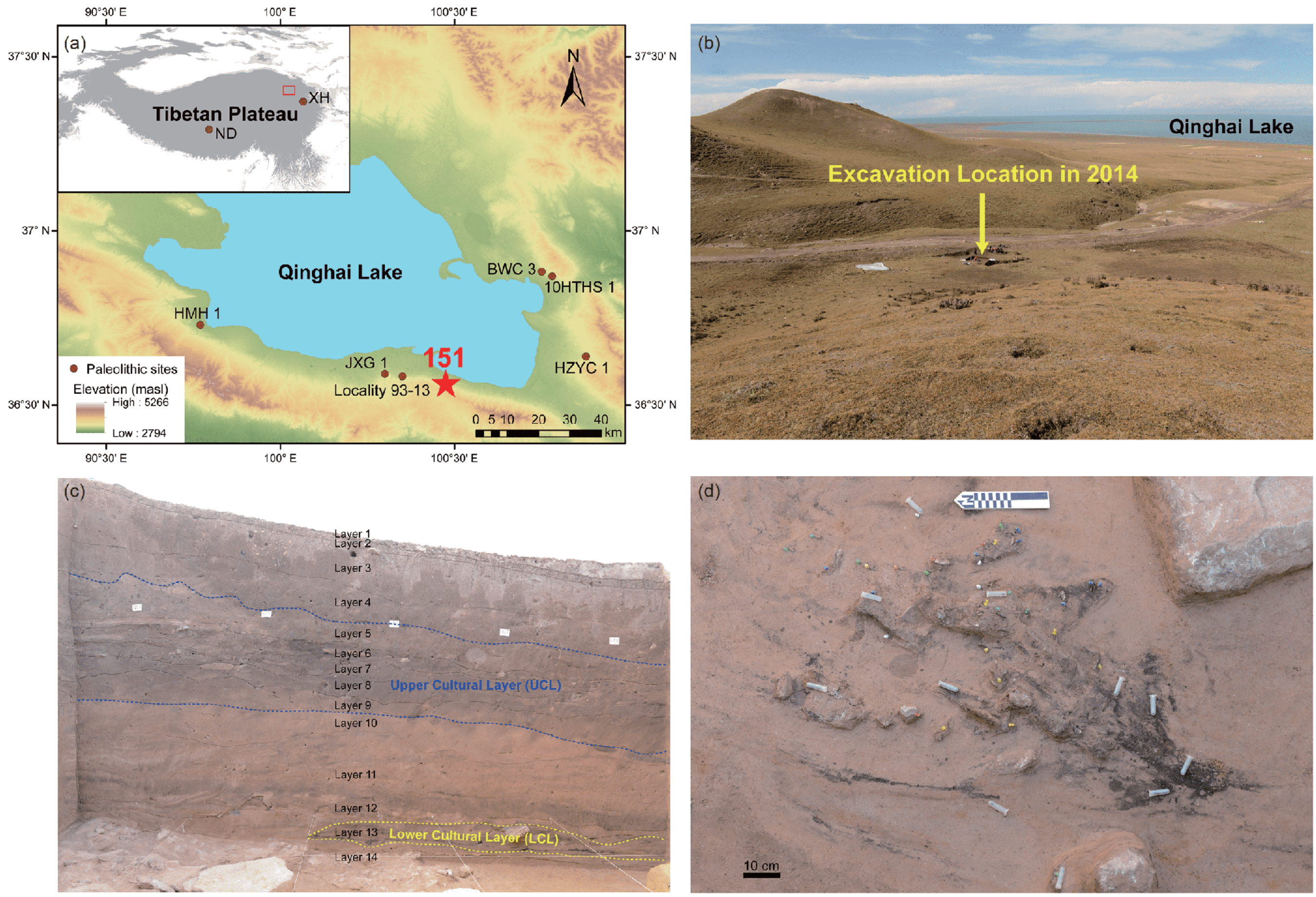

Figure 1 Qinhai Lake Basin and excavation of the "151 site". (a) Distribution of Paleolithic sites in the Qinghai Lake Basin during the Last Deglacial Period; (b) excavation location of the "151 site" in 2014; (c) profile of the west wall in the excavation; (d) overhead view of the hearth in LCL.

3. Materials and methods

3.1 AMS ^{14}C dating

We determined the age of the "151 site" LCL through five AMS radiocarbon dates for bones and charcoal samples. The extraction steps of collagen from bones followed Ma et al. (2016), and the pretreatment of charcoal follows the classical ABA (acid-base-acid) method (Haesaerts et al., 2013). Experiments and follow-up procedures such as graphitization were completed at the MOE Key Laboratory of Western China's Environmental System in Lanzhou University. AMS measurements were completed at Peking University. All dates provided in this paper are corrected to calendar age by IntCal13 calibration curve (Reimer et al., 2013) in OxCal 4.3 and expressed as cal yr BP.

3.2 Analysis methods of animal bones

During excavation, all archaeological remains were systematically collected. Three-dimensional coordinates for each bone bigger than 2 cm or smaller than 2 cm but with identification characteristics were recorded using a total station and then numbered and bagged. All soil from cultural layers was dry and wet sieved using 3 mm sieve. Floatation samples were also collected from each excavation units. All plant remains, animal remains, and stone artifacts were collected during sieving and floatation.

After excavation, all bones collected from sieving were further sieved with a 10-mm sieve in the MOE Key Laboratory of Western China's Environmental Systems in Lanzhou University. Then, all identifiable bones were identified using modern and ancient comparative collections in the laboratory at Lanzhou University. Because bones were extremely fragmentary, most of the identifiable bones were only identified to body size rather than specific species. These specimens were classified by body size into large ungulates (e.g. wild yak (*Bos grunniens*) and wild horse/ass (*Equus* sp.)), medium ungulates (e.g. red deer (*Cervus elaphus*)), small ungulates (e.g. Przewalskii's gazelle (*Procapra przewalskii*)), and small mammals (e.g. hare (*Lepus* sp.) and marmot (*Marmota* sp.)).

During identification, all recognizable bone specimens were identified, including skull, teeth, vertebrae, ribs, limb bones, phalanx bones, etc. In addition, unidentifiable fragments with maximum length ≥1 cm were counted. Precise skeletal elemental location or portion and completeness of identified specimens (i.e., percentage of the portion of the element represented) were recorded according to skeletal elements (Klein and Cruz-Uribe, 1984; Lyman, 1994). In the identification of limb bone fragments, diagnostic zones (Stiner, 2002) and other morphological characteristics (Barba and Domínguez-Rodrigo, 2005) were used to identify and quantify completeness. The age of death of horses was determined based on tooth eruption and wear (Fernandez and Legendre, 2003). The teeth of *Bos* were too broken to be used for age estimation. Faunal taphonomic analysis is used to understand animal assemblage formation and burial processes (Behrensmeyer, 1991; Lyman, 1994). Bone surface modifications caused by human activity (butchery, burning, and fracturing), animal gnawing (carnivore and rodent) and other agents (weathering, root activity, and trampling) (Behrensmeyer, 1978; Lyman, 1994; Blumenschine et al., 1996) were observed and recorded for each specimen through a 10×-magnifying lamp. Limb bone shaft fragment fracture types (i.e., broken when fresh or broken when dry) (Villa and Mahieu, 1991) and shaft circumference (Marean et al., 2004) were also recorded.

4. Results

4.1 AMS ^{14}C dating results

Five AMS ^{14}C dates have been obtained (Table 1). These reveal that the age range of the LCL at the "151 site" is 15400–13100 cal yr BP. The LCL occupation is contemporaneous with other sites like JXG 1 (14920–14200 cal yr BP), HMH 1 (13440–12410 cal yr BP) and HZYC 1 (13541–12877 cal yr BP) in the Qinghai Lake Basin (Madsen et al., 2006, 2017). Here radiocarbon dates of charcoal samples are slightly older than that of bone samples by about 400–1000 years, which is common in Paleolithic sites, probably due to the 'old wood' effect of charcoal samples (Zilhão and d'Errico, 1999; Jöris et al., 2003). Another explanation might be intermittent repeated short-term human occupations at the site.

4.2 Bone identification and analysis results

The total weight of bone remains in the LCL of the "151 site" is 445.9 g, with materials coming from 23 excavation units. The faunal assemblage is mainly composed of extremely broken ungulate bone shaft fragments and teeth fragments. Animal taxa were mainly identified based on the teeth. A total of 227 specimens bigger than 1 cm were collected. Out of those, the number of identifiable specimens (NISP) is 126, and the minimum number of individuals (MNI) is 4 (Table 2). Although the number of specimens in the LCL is small, poor bone preservation is a common situation at many Paleolithic single hearth sites (Vaquero and Pastó, 2001).

The LCL faunal assemblage is dominated by large ungulates (*Bos* and wild horse/ass) that make up over 90% of the assemblage. Small ungulates (Przewalskii's gazelle-sized) make up 9.5% of the assemblage. Only one small mammal bone was found, a metacarpal of the woolly hare (*Lepus oiostolus*) (Table 2). Remarkably, no carnivores were identified. Ungulates appear to have been the main target of hunting at the "151 site" LCL and other contemporaneous sites, such as JXG1 and HMH 1 in the Qinghai Lake Basin (Madsen et al., 2006). There is no evidence that a "Broad Spectrum Revolution" took place in the Qinghai Lake Basin during the Last Deglacial Period in the same way that it may have taken place in other regions of China (Zhang S Q et al., 2016).

Only one right second mandibular premolar (P2) with about 20 mm crown height from a wild horse/ass provided valid information about the age of death, revealing that the individual was an adult when it died.

5. Discussion

Zooarchaeological and taphonomic analysis of faunal remains from LCL of the "151 site" provide important information for our understanding of Paleolithic site formation, human subsistence strategies and adaptation to high-altitude environments on the Tibetan Plateau during the Last Deglacial Period.

5.1 Faunal taphonomy

Taphonomic analyses of archaeological bone assemblages play an important role in studies of site sedimentary history and human subsistence strategies. From biosphere to lithosphere, archaeological faunal assemblages are influenced not only by natural factors including weathering, decomposition, dissolution, compaction, petrification, carnivore and rodent gnawing, and so on, but also by human activities including acquisition, transportation, processing, and consumption of animals (Lyman, 1994). Therefore, the formation of archaeological faunal assemblages are usually a complex and comprehensive process. Taphonomy should be studied before interpreting human behaviors reflected in faunal assemblages from archaeological sites.

Bone aggregation in the LCL by rodents (Brain, 1981) and raptors (Andrews, 1990) is unlikely given the taxonomic composition, which is dominated by ungulates, and the spatial distribution of bones, which is concentrated in the hearth feature. In addition, the lack of carnivore and rodent modifications (Table 3) and digestive traces on bone surfaces also indicates that carnivores, rodents, and raptors were not

Table 1 AMS radiocarbon dates for Lower Cultural Layer in the "151 site"

Lab number	Dated material	^{14}C age (yr BP)	Calibrated age (cal yr BP)	
			1δ	2δ
LZU14284	Charcoal	12920±35	15420±105	15438±188
LZU16244	Charcoal	12265±35	14159.5±67.5	14188.5±162.5
LZU14285	Charcoal	12150±40	14040±65	14010.5±153.5
LZU16291	Bone	11895±35	13699±72	13680±101
LZU16292	Bone	11300±40	13142.5±45.5	13159±89

Table 2 Skeletal elements identified by taxon at the "151 site" LCL[a)]

Skeletal elements		*Bos* sp.	*Equus* sp.	Large ungulates	Small ungulates	*Lepus oiostolus*
Head	Skull frag.			1		
	Maxilla			1		
	Mandible frag.			3	1	
	Mandibular teeth	1	3			
Body	Cervical vertebrae			1		
	Vertebrae				1	
	Rib frag.			20	5	
Forelimb	Scapula					
	Humerus, pro/dis/sh	0/0/2		0/0/1		
	Radius, pro/dis/sh			0/0/1		
	Ulna, pro/dis/sh					
	Metacarpal, pro/dis/sh					1*
Hindlimb	Pelvis				1	
	Femur, pro/dis/sh					
	Tibia, pro/dis/sh			0/0/2	0/0/1	
	Metatarsal, pro/dis/sh					
Toes	Phalanx 3, pro/dis				1/0	
	Indet. teeth frag.			34		
	Indet. long bone frag.			43	3	
	NISP	3	3	107	12	1
	MNI	1	1		1	1
	%NISP	2.4	2.4	84.9	9.5	0.8

a) pro, proximal; dis, distal; sh, shaft; frag., fragment; indet., indeterminate. Large ungulates include *Bos* and wild horse/ass specimens. Small ungulates are the size of Przewalskii's gazelle. * indicates complete bone elements.

involved in bone aggregation. The "151 site" is located at the bottom of a hill slope, and it seems that slope fluvial transportation affected bone distribution during and after deposition. Generally, fluvial transportation transforms existing bone assemblages rather than aggregating bones in primary deposits (Behrensmeyer, 1978). In the LCL, 23.78% (NISP=29) of bone surfaces show fluvial abrasion modifications. Charcoal distribution in and around the hearth is in bands along the slope (Figure 1d), indicating slight fluvial transportation took place. However, stone artifacts and bones were not influenced much by the weak fluvial transportation as they remain distributed around the hearth (Figure 1d). The above observations suggest that the faunal assemblage from the LCL is mainly a result of human activities and has not been affected much by other natural factors before, during, or after deposition.

5.2 Human subsistence strategy

In terms of primary spatial utilization characteristics for prehistoric and modern hunter-gatherers, hearths usually were core features at prehistoric archaeological sites that tied individuals together in hunter-gatherer groups (O'Connell, 1987; O'Connell et al., 1991; Vaquero and Pastó, 2001). As early as the Middle Paleolithic, hunter-gatherers carried out a series of activities around hearths, including food processing and sharing, tool production and maintenance, and much more (Stiner et al., 2009). Hearth size is a good proxy to

Table 3 Bone-surface modifications and bone fracture patterns for ungulate groups[a)]

Bone-surface modifications and fracture patterns		Large ungulates	Small ungulates
Burning	n	2	7
	%	2.7	58.3
Green fracture	n	30	2
Dry fracture	n	14	0
Intermediate fracture	n	1	0
Limb shaft circumference	<50%	45	2
	>50%	0	0
	100%	0	0
Weathering (stage 3–5)	n	68	2
	%	90.7	16.7
Cut-marks	n	2	1
	%	2.7	8.3
Percussion marks	n	0	0
	%	0	0
Gnawing (carnivore)	n	0	0
	%	0	0
Gnawing (rodent)	n	0	0
	%	0	0
Root-marks	n	4	1
	%	5.3	8.3
Trampling striations	n	0	0
	%	0	0

a) Bone-surface modifications and bone fracture patterns for ungulates. Teeth and teeth fragments are not included. NISP of large and small ungulates are 75 and 12, respectively.

estimate group size, which contributes to our understanding of human subsistence strategies. During consumption and production activities around hearths, individual numbers are limited by the size of hearths, as each individual must occupy a certain size of space. Therefore, prehistoric hunter-gatherer group sizes could be inferred from hearth sizes. Human activity ranges are usually a circular region with a radius of about 1.75 m around the center of a hearth (Binford, 1996). Usually, an individual takes up an activity area of about 2.5–3 m^2 (Freeman, 1978) or resembling a circular area with a diameter of about 1.80–1.94 m (Henry, 2012). Based on the above estimates, it can be inferred that the hearth with a diameter of about 1 m in the LCL was suitable for a single family scale group of 1–5 people and it would have been overcrowded if more than 5 people were sitting at the hearth. The size of this hearth is similar to hearths found in other contemporaneous sites in the basin such as JXG 1, HMH 1 and Locality 93-13, which are also between 0.5 and 1.5 m (Madsen et al., 2006, 2017). These hearths match the range of short-term campsite hearths of modern hunter-gatherers, much smaller than hearths used by large groups in modern hunter-gatherer societies (Yellen, 1977). Therefore, hearth features found in these sites suggest that the ancient population size was small and that short-term human activities dominated in the Qinghai Lake Basin during the Last Deglacial Period.

Skeletal element representation analysis can provide important human behavioral information relating to the acquiring, processing, and transporting of animal carcass portions. The small ungulate remains are too few (NISP=12) to conduct in-depth skeletal elemental analysis. Skeletal element distributions for large ungulates (primarily *Bos* and wild horse/ass) (Table 2) suggests that hunter-gatherers might selectively transported carcass parts. They probably chose to bring back meat-heavy upper (femur and humerus), intermediate limb bones (tibia and radius-ulna) and torsos (vertebra and ribs) to campsite for further processing and consumption. Large ungulates (e.g. *Bos*) are usually too big to be carried back to camp site intact. Therefore, it is common for hunter-gatherers to chop off the horns from the head, remove the internal organs, and dismember the carcass into several large anatomical units (usually the limbs are dismembered separately) at kill sites before transporting certain carcass parts back to campsites (Bunn et al., 1986). Even though the skull and torso have a low Standardized Food Utility Index compared with limb bones (Lyman, 1994), there are usually still a lot of nutrients remaining on these portions of the skeleton after preliminary meat and marrow extraction at kill sites (Marean and Cleghorn, 2003). The presence of maxillary and mandibular teeth, cervical vertebrae, and a large number of rib fragments of large ungulates indicates that in order to avoid the waste of nutrients in heads and torsos, hunter-gatherers probably chose to bring these carcass parts back to campsite for more thorough nutrient processing. This pattern is consistent with modern Hadza hunter-gatherers who maintain a balance between nutrient income and transportation cost (Lupo, 2006).

Transporting carcasses is not an easy job for hunters. Although a hunter can carry up to 25–30 kg of prey, teamwork by up to 24 hunters is needed to transport a complete 35–40 kg buffalo leg including a subsidiary organization back to a campsite about 5 km away, and repeated rest and replenishing are also needed during transportation (Hall, 2007). Even to transport a much smaller wild horse, cooperation of several hunters is needed to transport the whole carcass (Binforn, 1978; Bunn, 1993). However, hunters only need to choose whether to bring the complete carcass or parts of the carcass back to their campsite when the carrying distance is long or the hunter group is very small. In the case of the small population at the "151 site", people decided to transport both heads and torsos back to the campsite, indicating that the kill site may not have been far away. Considering that *Bos* and *Equus* are highly dependent on water and that "151 site" is located next to a small river, it can be inferred that humans might have hunted these large animals near their campsite.

Bone-surface modifications and fracture patterns can also provide important information about human behavior. Bone-surface modification analysis of the LCL animal bones indicates that large ungulate bones were much more weathered than small ungulate bones before burial (Table 3). Perhaps it took longer for the larger bones to become buried, leaving the larger bones outside for longer weathering times. Of course, it is also possible that large and small ungulates were brought back to the site after different hunting events. According to long bone shaft fracture patterns (fracture outline and fracture texture) of ungulates (Villa and Mahieu, 1991), the long bones from LCL were usually broken fresh (Table 3), indicating a bone marrow extraction behavior. Bone grease might also have been extracted through a "Hot Stone Boiling" method (Lupo, 1995), which is implied by the large number of fire-cracked stones, long bone shaft fragments, and the absence of long bone epiphyses (Table 2). Animal fat and grease are important for human diets, especially for lactating women and children (Burger et al., 2005), due to their high energy and long storage time (Vehik, 1977). Many fire-cracked stones and long bone shaft fragments of ungulates have also been found in the contemporary JXG 1 and HMH 1 sites (Madsen et al., 2006). We conclude that intensive utilization of animal resources was widely practiced by the Last Deglacial hunter-gatherers in the Qinghai Lake Basin in order to meet the high energy demands for living in cold and high elevation environments. Though, the ubiquitous phenomenon of high degree of bone breakage at the contemporaneous sites, but it is still hard to say with certainty whether bone grease extraction took place.

5.3 Environmental adaptation strategy

Faunal remains from the LCL of the "151 site" and other contemporaneous sites in the Qinghai Lake Basin during the Last Deglaciation are all dominated by ungulates, but their prey compositions are very different. The faunal assemblage of "151 site" is mainly composed of large ungulates (*Bos* and *Equus*), while JXG 1 and HMH 1 are dominated by small ungulates of gazelle body-size (Madsen et al., 2006). Dietary breadth models of optimal foraging theory (Smith et al., 1983) indicate that humans, like other animals, are expected to maximize energy obtained in foraging processes, which means that they will preferentially hunt high-ranked animals such as ungulates, or expend very limited energy to capture low-cost animals such as turtles (Winterhalder, 1986). The dominance of high-ranked ungulates in Last Deglacial sites in the Qinghai Lake Basin suggests that small-scale populations with short-term occupations had not yet depleted high-ranked animals in the basin (Stiner, 2002). These hunter-gatherers might have conducted opportunistic hunting of high-ranked ungulates following the predictions of optimal foraging theory (Bunn, 2001) in order to meet short-term living needs of small-scale groups. It is also possible that hunter-gatherer groups living in different regions used different subsistence strategies under the same technical conditions. In addition, the emergence of several contemporaneous sites with short-term occupations indicates that hunter-gatherers adopted a high residential migration strategy (Kelly et al., 2005) in the Qinghai Lake Basin during the Last Deglacial Period.

The sudden appearance of small-scale and highly-mobile hunter-gatherers in the Qinghai Lake Basin during the Last Deglacial Period might have resulted from the gradually ameliorating climate as well as technological innovation. An increase in temperature and precipitation (Yu and Kelts, 2002; Colman et al., 2007), turnover of vegetation from desert steppe to alpine meadow/subalpine shrub (Shen et al., 2005), and recovery of animal population on the Tibetan Plateau created more food resources and space for hunter-gatherers. At the same time, microlithic technology, which is generally considered to be closely related to highly mobile hunting activities in harsh environments, started to become more common in North China along with other effective tools for safer hunting of large animals, complex hide garment manufacturing, and sewing (Yi et al., 2016). Therefore, microlithic tools are very helpful for humans dealing with unfavorable high-altitude environments, such as the relative shortage of food resources and big temperature variations during the day, by increasing hunting success and clothes manufacturing. In addition, the quality of resource patches greatly varies according to the large climate changes between seasons on the Tibetan Plateau, which means more predictable seasonal resources, higher hunting success rates and greater attractiveness to hunter-gatherers. However, the significant seasonal climate differences also mean harsher environments and fewer food resources in winter and spring (Shi et al., 2006), probably forcing hunter-gatherers to move down to low-altitude regions, making it unlikely that people were able to occupy the plateau year-round (Zhang D J et al., 2016, 2017).

6. Conclusion

The discovery of the LCL of the "151 site" in Qinghai Lake Basin enriches our understanding of hunter-gatherer activities on the high-altitude Tibetan Plateau during the Last Deglacial Period. Taphonomic and zooarchaeological studies of animal remains of this site reveal human transportation and utilization strategies of animal resources. In terms of transportation, people chose to transport the high nutritional upper and intermediate limb bones, heads and torsos of large ungulates back to campsite for further processing and consumption. In terms of utilization, besides meat, ancient humans also extracted bone marrow and even bone grease, indicating intensive animal resource utilization that may have been a necessary adaptation when living in an environment with limited resources such as the high-altitude plateau. We found that short-occupation sites in the Qinghai Lake Basin at the end of Pleistocene consisted of scattered hearth features containing faunal assemblages dominated by ungulates of various body-sizes. Our study shows that small-scale and highly mobile hunter-gatherer groups intermittently occupied the Qinghai Lake Basin during the Last Deglacial Period, relying on opportunistic hunting of high-ranked ungulates in order to adapt to high-energy demanding and significant seasonal environments on the Tibetan Plateau.

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