

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/341312669>

Early commensal interaction between humans and hares in Neolithic northern China

Article in *Antiquity* · May 2020

DOI: 10.15184/aqy.2020.36

CITATIONS

0

READS

198

7 authors, including:



Sheng Pengfei

Fudan University

8 PUBLICATIONS 5 CITATIONS

[SEE PROFILE](#)



Yaowu Hu

Chinese Academy of Sciences

40 PUBLICATIONS 727 CITATIONS

[SEE PROFILE](#)



Xue Shang

Chinese Academy of Sciences

17 PUBLICATIONS 282 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



archaeology [View project](#)




Agricultural economy around Shimao [View project](#)



Research Article

Early commensal interaction between humans and hares in Neolithic northern China

Pengfei Sheng^{1,2} , Yaowu Hu^{1,2}, Zhouyong Sun³, Liping Yang³, Songmei Hu³, Benjamin T. Fuller⁴ & Xue Shang^{5,6,*}

¹ Institute of Archaeological Science, Fudan University, P.R. China

² Department of Cultural Heritage and Museology, Fudan University, P.R. China

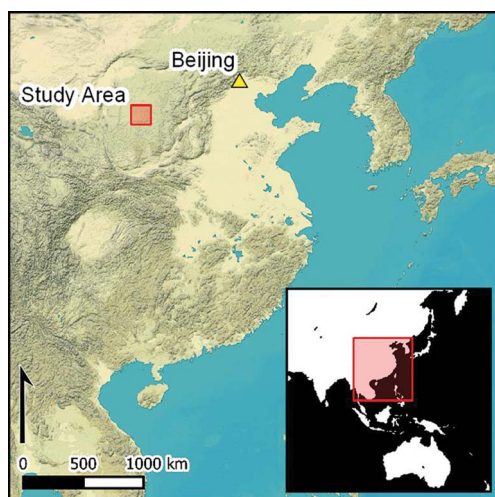
³ Shaanxi Provincial Institute of Archaeology, Xi'an, P.R. China

⁴ Department of Archaeology and Heritage Studies, Aarhus University, Denmark

⁵ Department of Archaeology and Anthropology, University of Chinese Academy of Sciences, Beijing, P.R. China

⁶ Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, P.R. China

* Author for correspondence: ✉ shangxue@ucas.ac.cn



Human influence on ecological niches can drive rapid changes in the diet, behaviour and evolutionary trajectories of small mammals. Archaeological evidence from the Late Neolithic Loess Plateau of northern China suggests that the expansion of millet cultivation created new selective pressures, attracting small mammals to fields and settlements. Here, the authors present direct evidence for commensal behaviour in desert hares (*Lepus capensis*), dating to c. 4900 years ago. Stable isotope ratio analysis of hare bones from the Neolithic site at Yangjiesha shows a diachronic increase in a C₄ (millet-based) diet, revealing, for the first time, the expansion of ancient human-hare interactions beyond the predator-prey relationship.

Keywords: China, Loess Plateau, leporids, commensalism, human ecology, stable isotope analysis

Introduction

The domestication of a select number of plant and animal species has transformed human interactions with a multitude of other, non-domesticated plants and animals (Fuller & Stevens 2017; Turcotte *et al.* 2017). Specifically, food-production systems have created new niches for animals, instigating commensal interactions—that is, animals benefiting from a relationship with humans, which neither benefits nor harms the latter—which, in turn, may influence faunal evolutionary trajectories. Recent research in the Levant, for example, has found that house mice (*Mus musculus domesticus*) that consumed the midden waste of

Received: 11 April 2019; Revised: 4 August 2019; Accepted: 14 August 2019

© Antiquity Publications Ltd, 2020

hunter-gatherers 15 000 years ago had a competitive advantage over other mice (Weissbrod *et al.* 2017). Mouse-human commensalism therefore demonstrates evolutionary effects on mice, but the evolutionary influence of agriculture-related commensalism on other smaller mammal species remains unclear. Archaeological consideration of such animals, particularly agricultural pests such as rabbits that opportunistically consume crops but generally do not enter human settlements, may provide new insights into the influence of commensalism on evolutionary pathways. Although archaeologists have found evidence for a predator-prey relationship between humans and leporids (rabbits and hares) as early as the Late Palaeolithic as part of broadening dietary practices (e.g. Hockette & Haws 2002; Aura *et al.* 2009; Lloveras *et al.* 2016), there is limited archaeological evidence for commensal or other relationships between humans and leporids.

The earliest evidence for close human-hare interactions comes from an Early Copper Age (mid fifth millennium BC) burial in Hungary, in which an adult European brown hare (*Lepus europaeus*) was interred with an older woman (Bartosiewicz *et al.* 2013); and in Sweden, archaeologists have discovered 12 hare (*Lepus timidus*) metapodials from a third-millennium BC grave at Ajvide (Mannermaa 2008). Meanwhile, at Teotihuacan in the Mexico Basin c. AD 1–550, carbon and nitrogen stable isotope analysis has revealed that cottontails (*Lepus sylvaticus*) and jackrabbits (*Lepus timidus*), probably tamed, consumed some plants produced by humans (Somerville *et al.* 2017). This suggests that isotopic analysis of hares can be used to document expansion or change in past agrarian systems and settlement structures.

Due to their wide geographic range, adaptability and frequent presence on archaeological sites, desert hares (*Lepus capensis*) are an ideal species to investigate the possible influence of cereal agriculture on the evolutionary trajectories of small mammals. They are widely distributed in the Eurasian Steppe and desert areas, and adapt easily to a broad range of environmental conditions. Their geographic range includes most of China's northern provinces, including Shaanxi, Shanxi, the northern part of Xinjiang, and Inner Mongolia. Desert hares feed on herbaceous plants, such as Gramineae and chenopods. When food is scarce, they will also eat the tender leaves of crops, as well as some seeds. Moreover, their skeletal remains are particularly abundant on archaeological sites in China. Archaeological evidence of a human-hare predator-prey relationship on the Loess Plateau dates to as early as the Late Pleistocene (Zhang *et al.* 2016); and in the Late Neolithic, desert hares account for a large proportion (approximately 40 per cent, based on the minimum number of individuals (MNI)) of the faunal assemblages from some sites on the northern Loess Plateau (e.g. Hu *et al.* 2013). This suggests that humans exploited hares for their meat and fur, and possibly kept them in captivity.

Most of the Holocene evidence for human-hare interactions reveals that humans assigned religious and spiritual significance to hares, as is also attested in art and literature. Excavations in northern China have yielded symbolic representations of leporids in the form of jade carvings and bronze decorations, from the Bronze Age onwards (Figures 1a–b) (The Institute of Archaeology, CASS 1982: 92; Gu 2005: 68; Shaanxi Institute of Archaeology Research 2009: 735–38). Moreover, the first oracle bone texts and the *Shijing* (*The Book of Odes*, eleventh to seventh centuries BC) detail ritual practices related to hare hunting (Figure 1c–d) (Legge 1876: 63; The Institute of Archaeology, CASS 2003: 795). From the Han Dynasty (202 BC–AD 220) onwards, leporids were regarded as an auspicious

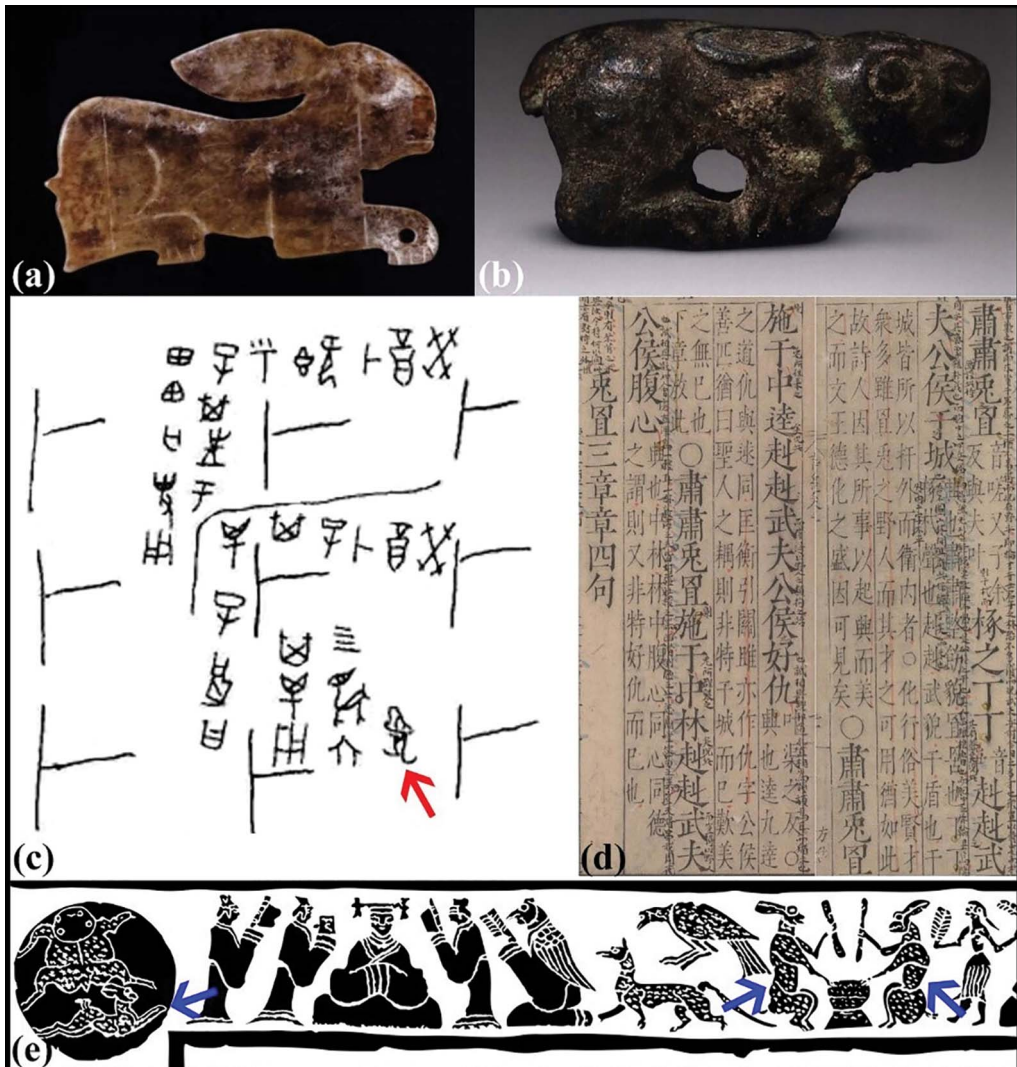


Figure 1. a) Jade carving of a rabbit from a Western Zhou Dynasty (1046–771 BC) tomb in Shaanxi Province; b) bronze ornament for a chariot in the shape of a rabbit from Lijiapancun, a site dating to the Warring States period (475–221 BC) in Shaanxi Province; c) an oracle bone from Yinxu (c. 1300–1100 BC); the red arrow shows the character for rabbit; d) writings about rabbit hunting in the *Shijing* book (c. 500 BC) (<https://shuge.org/ebook/shi-jing-ji-zhuan>); e) stone relief with leporid symbolism related to the Moon (left, blue arrow) and female herbalists (right, blue arrows) from a Han Dynasty tomb (AD 92) in Shaanxi Province (figure by P. Sheng).

animal described in myths and depicted on stone reliefs, or represented by the moon (Figure 1e) (Li & Wang 2001: 18–20). While humans clearly had complex interactions with leporids in China from the Bronze Age onwards, there is still little evidence documenting how an increasingly agrarian landscape may have affected the diet and behaviour of hares.

Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratio analysis allows us to investigate the nature and scale of long-term interactions between humans and animals (e.g. Hu *et al.* 2014;

Hu 2018). This method provides a direct reconstruction of dietary patterns, making it possible to observe diachronic changes in diet resulting from the expansion of agricultural practices (Somerville *et al.* 2017). Although people in northern China have cultivated common millet (*Panicum miliaceum*) and foxtail millet (*Setaria italica*) since the Early Neolithic (Zhao 2011), human-hare co-evolutionary interactions, particularly in the context of the Late Neolithic expansion of millet agriculture, have yet to be investigated.

In this article, we investigate how the desert hare in northern China's Loess Plateau was affected by agricultural activities in the Neolithic, and attempt to determine how human-hare interactions broadened over time as a result of the expansion of millet agriculture. The northern Loess Plateau is located in the transitional zone from the hilly area of the Loess Plateau to the Mu Us Sand Field (106°10'–110°30' east, 37°28'–39°23' north; Figure 2a). In this region, we seek to identify whether some hares received special care, such as being fed on cultivated millets. To do so, we present $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ results for humans ($n = 4$), hares ($n = 54$) and other animals ($n = 33$) from two contemporaneous sites radiocarbon-dated to approximately 2800–2900 cal BC: Yangjiesha (areas A, B and C) (109°14' east, 38°02' north) and Wangyangpan (109°14' east, 38°03' north) (Figure 2b–d).

Materials and methods

Isotopic measurements

Collagen was extracted from four humans and 87 animals, including desert hares (Figure 3), at the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences, following the protocol outlined in Richards and Hedges (1999), and modified to include a final ultrafiltration stage prior to lyophilisation (Brown *et al.* 1988). Detailed information concerning the archaeological contexts of the samples is listed in Table S1 in the online supplementary material (OSM).

Purified collagen was measured at the Department of Archaeology and Anthropology at the Chinese Academy of Sciences, using an IsoPrime 100 IRMS (Elementar, UK) coupled with an Elementar Vario (Elementar, UK), with the sulfanilamides listed in the OSM as reference materials. For every 10 samples, a standard collagen sample ($\delta^{13}\text{C} = -14.7 \pm 0.2\text{‰}$; $\delta^{15}\text{N} = 7.0 \pm 0.2\text{‰}$) was inserted for calibration and to monitor stability. The results were analysed as the ratio of the heavier isotope to the lighter isotope ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$), and expressed as 'δ' in parts per 1000 (‰), relative to internationally defined standards (Lee-Thorp 2008) for carbon and nitrogen. We utilised two-point calibrations (Szpak *et al.* 2017). The measurement errors were less than $\pm 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Radiocarbon dating

Bone samples were collected from two desert hares recovered from two pits at the Yangjiesha site (Figure 2d) and were dated by AMS at Beta Analytic Inc., Miami, USA. The dates were calibrated using the OxCal v4.3 programme and the IntCal13 calibration curve (Bronk Ramsey 2009; Reimer *et al.* 2013).

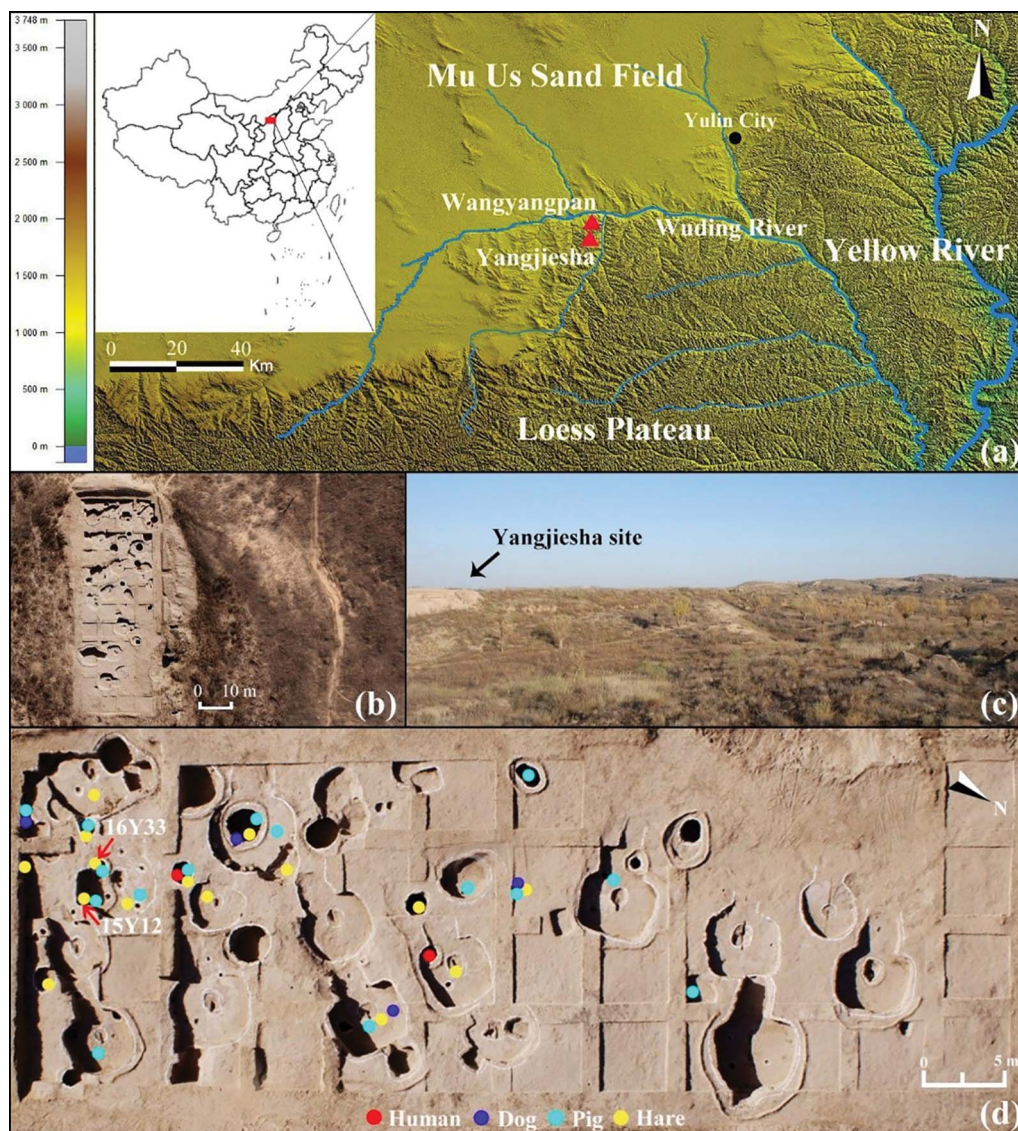


Figure 2. a) Map of the study area and sampled sites mentioned; b) overview of area A at Yangjiesha; c) natural landscape around Yangjiesha (arrow); d) locations of the specimens studied from the excavations at Yangjiesha; the locations of the two hare samples that were radiocarbon-dated (15Y12 and 16Y33) are indicated by red arrows (map by P. Sheng and photographs provided by Liping Yang).

Results

Isotopic analysis

All human and animal specimens from the sites of Yangjiesha and Wangyangpan produced good quality collagen, with C:N ratios between 2.9 and 3.6 (DeNiro 1985; Ambrose 1990), suggesting that the samples were well preserved and suitable for interpretation. The range of



Figure 3. Skull of a desert hare (*Lepus capensis*) from Yangjiesha (photograph provided by S. Hu).

(-19.0‰ to -6.1‰) and $\delta^{15}\text{N}$ values (5.5‰ to 9.1‰). While the majority of pigs consumed C_4 -based foods, three individuals had low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, suggesting either that they were wild, or were domestic pigs which were fed only C_3 -based diets (local terrestrial plants, grasses and shrubs).

Desert hares

The 54 samples of desert hare show a wide distribution of isotopic values, with $\delta^{13}\text{C}$ ranging from -21.5‰ to -13.9‰ , and $\delta^{15}\text{N}$ ranging from 2.2‰ to 7.2‰ (see Figure 4). Previous studies have used a $\delta^{13}\text{C}$ cut-off value of approximately -18.0‰ as the general transition between predominantly C_3 and mixed C_3/C_4 diets (Wang *et al.* 2017). Most hares (80 per cent) have $\delta^{13}\text{C}$ values $< -18.0\text{‰}$, that is, their diet was C_3 -based. The remaining 20 per cent (11 specimens) had a mixed C_3/C_4 diet. Specimen 16Y33, in particular, has the most ^{13}C -enriched (-13.9‰) and ^{15}N -enriched (7.2‰) values of all the desert hares analysed (Table S1). Two specimens were also

‰C and ‰N results are $32.4\text{--}49.7\%$ and $11.8\text{--}19.2\%$, respectively. The sample information and isotopic results are summarised in Table S1 and plotted in Figure 4.

Humans

The range of human ($n = 4$) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are -10.7‰ to -6.0‰ and 7.7‰ to 10.5‰ , respectively. The three adults all have ^{13}C -enriched results indicative of the consumption of C_4 diets (foxtail and common millet). The $\delta^{15}\text{N}$ values for the humans are similar to those for pigs and dogs, which suggests that they all consumed similar foods. Additionally, the single human infant analysed produced a lower $\delta^{13}\text{C}$ value (-10.7‰) and a higher $\delta^{15}\text{N}$ value (10.5‰) in comparison with the adults.

Domestic animals

The dog samples ($n = 6$) have mean $\pm\text{SD}$ $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of $-7.2\pm 0.7\text{‰}$ and $7.5\pm 0.8\text{‰}$, respectively. This indicates that the dogs' diet was heavily influenced by C_4 -based protein. The pigs ($n = 27$) show a wide range of $\delta^{13}\text{C}$

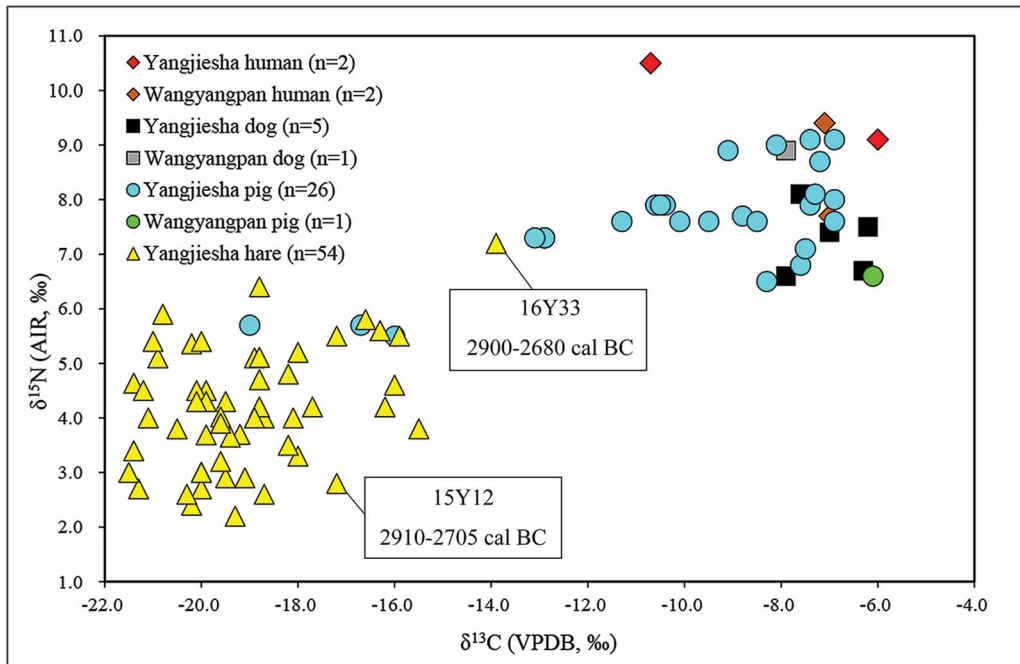


Figure 4. Human and animal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from Yangjiesha and Wangyangpan, with radiocarbon dates of two hares (figure by P. Sheng).

selected for AMS radiocarbon measurements: 15Y12 dated to 2910–2705 cal BC and 16Y33 dated to 2900–2680 cal BC (95.4% confidence) (Table 1).

Discussion

As habitats exert strong selective pressures on small mammals, human manipulation of these animals' ecological niches can result in rapid changes in diet, behaviour and possibly even evolutionary trajectories (Wu & Drozdov 2016; Fuller & Stevens 2017). Archaeological evidence indicates that the wide distribution of millet farming and increased agricultural food production on the Loess Plateau during the Late Neolithic introduced a new suite of selective pressures, attracting small mammals to this newly created ^{13}C -enriched niche in a C_3 plant-based environment (Liu *et al.* 2011; Dong *et al.* 2016). In support of this, isotopic studies of mammals that lived on the Loess Plateau have found ^{13}C -enriched values for some small mammal species (Tables 2–3 & Figure 5). A Chinese zokor (*Myospalax* sp., a rodent) found at Quanhucun (3500–3200 BC), for example, had a $\delta^{13}\text{C}$ of -8.5‰ value, which was very close to that of dog and pig specimens fed on millet foods in the same archaeological contexts, suggesting that it had probably consumed millet products or prepared foods (Hu *et al.* 2014). Elevated $\delta^{13}\text{C}$ values were also observed in a Chinese zokor (-11.6‰) and rat (*Rattus norvegicus*) (-9.3‰) from the Late Neolithic site of Wuzhuangguoliang (c. 3000 BC) (Guan *et al.* 2008). This indicates that rodents probably consumed large quantities of millet or millet-based foods in human-controlled environments. Furthermore, cats

Table 1. Radiocarbon dating of desert hares (*Lepus capensis*). Radiocarbon dates were calibrated using the OxCal v4.3 program and IntCal13 calibration curve (Bronk Ramsey 2009; Reimer et al. 2013).

Lab. no.	Sample ID	Sample type	Radiocarbon (years BP)	Cal BC (95.4% confidence)	Percentage probability (%)
Beta-465232	16Y33	Hare bone	4210±30	2900–2850	35.2
				2815–2740	49.9
				2730–2690	13.9
				2690–2680	0.1
				Median age probability = 2795 cal BC	
Beta-465233	15Y12	Hare bone	4240±30	2910–2860	71.8
				2819–2755	25.0
				2720–2705	0.3
				Median age probability = 2880 cal BC	

(*Felis* sp.) living at the Quanhucun site were attracted by commensal small mammals in human settlements and were subsequently kept by farmers to control the rodent population (Hu et al. 2014). In addition to these mammals, a pheasant (*Gallus* sp.) from the Dongying site had relative high $\delta^{13}\text{C}$ values of -12.0‰ , suggesting a large intake of C_4 -based foods (such as foxtail and common millet crops) between c. 2600 and 2000 BC (Chen et al. 2014) (Figure 5).

The desert hares analysed here show a wide range of $\delta^{13}\text{C}$ values, indicating that they had a varied diet (see Figure 4). The results suggest that most of the hares relied on C_3 foods, supporting Liu et al.'s (2011) hypothesis that C_3 plants dominated the vegetation surrounding the northern part of the Loess Plateau. A possible explanation for the abundant remains of hares consuming C_3 plants at Yangjiesha is that they were probably hunted at some distance from agricultural areas. This C_3 feeding behaviour is similar to previously published isotopic data for hares in Neolithic northern China (Figure 5 & Table 3). The hare (*Lepus* sp.) recovered from Xinglonggou (6200–5400 BC), for example, shows a very low $\delta^{13}\text{C}$ value (-23.5‰); at Quanhucun (3500–3200 BC), the value increases to -20.1‰ . The desert hares discovered at Xiahe (c. 3300–2700 BC) and Wuzhuangguoliang (c. 3000 BC) have a mean $\pm\text{SD}$ $\delta^{13}\text{C}$ value of $-18.6\pm 0.5\text{‰}$ ($n = 5$) (Table 3).

It is notable that 11 of the 54 (20 per cent) desert hare specimens from Yangjiesha have $\delta^{13}\text{C}$ values greater than -18.0‰ , indicating that they consumed a diet rich in C_4 plants. Notably, hares (*Lepus* cf. *capensis*) from the nearby sites of Dongying in the Wei River basin and Shimao, an early city on the northern Loess Plateau, also exhibit high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, from c. 2600–1800 BC (Figures 5–6 & Table 3). Both sites were probably surrounded by small agricultural villages that cultivated predominantly millets (*Panicum miliaceum* and *Setaria italica*, i.e. C_4 plants) (Jaang et al. 2018; Figure 6). Hence, the local ecology surrounding most ancient villages in northern China was C_4 -dominated (Bao et al. 2018; Sheng et al. 2018). We reason that the most likely explanation for this increase in the isotopic values of hares is due to the expansion of millet agriculture throughout Neolithic northern China (Dong et al. 2016; Bao et al. 2018; Sheng et al. 2018).

Table 2. Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for humans, domesticates, and wild animals from sites on the Loess Plateau around 3000 BC.

Species	Dating	n	$\delta^{13}\text{C} \pm \text{SD}$ (‰)	$\delta^{15}\text{N} \pm \text{SD}$ (‰)	References
<i>Homo sapiens</i>	3000 BC	10	-8.2 ± 1.8	9.5 ± 1.0	Hu <i>et al.</i> (2014); Chen <i>et al.</i> (2014); present study
<i>Sus scrofa</i>	3000 BC	51	-9.5 ± 2.9	7.7 ± 1.0	Hu <i>et al.</i> (2014); Chen <i>et al.</i> (2014); Guan <i>et al.</i> (2008); present study
<i>Canis familiaris</i>	3000 BC	13	-8.2 ± 2.1	7.7 ± 1.1	Hu <i>et al.</i> (2014); Chen <i>et al.</i> (2014); Guan <i>et al.</i> (2008); present study
<i>Cervus nippon</i>	3000 BC	8	-20.7 ± 1.4	4.1 ± 1.0	Hu <i>et al.</i> (2014); Chen <i>et al.</i> (2014)
<i>Myospalax</i> sp.	3500–3200 BC	1	-8.5	8.5	Hu <i>et al.</i> (2014)
	3000 BC	1	-11.6	5.3	Guan <i>et al.</i> (2008)
<i>Rattus norvegicus</i>	3000 BC	1	-9.3	6.9	
<i>Felis</i> sp.	3500–3200 BC	3	-12.3	5.8	Hu <i>et al.</i> (2014)
			-16.1	8.2	
			-13.5	8.9	
<i>Gallus</i> sp.	2600–2000 BC	1	-12.0	5.5	Chen <i>et al.</i> (2014)

While most hares on the Loess Plateau had diets consisting entirely of C_3 plants (in an area that was naturally dominated by these plants) (Liu *et al.* 2011), evidence for several ^{13}C -enriched desert hares from Yangjiesha suggests a long-term pattern of millet (C_4)

Table 3. Extant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of hares from sites in northern China.

No. in Figure 5	Site	Geographic coordinates	Dating	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	References
1	Xinglonggou	120°42'53"E, 42°21'57"N	6200–5400 BC	-23.5	1.4	Liu <i>et al.</i> (2012)
6	Quanhucun	109°51'40"E, 34°32'53"N	3500–3200 BC	-20.1	4.4	Hu <i>et al.</i> (2014)
7	Xiahe	109°35'4"E, 35°10'36"N	3300–2700 BC	-18.6 -18.8	2.3 5.2	Wang <i>et al.</i> (2018)
4	Wuzhuanguoliang	109°2'46"E, 37°48'35"N	3000 BC	-18.0 -18.4 -19.3	5.0 4.8 4.8	Guan <i>et al.</i> (2008)
5	Dongying	109°1'17"E, 34°27'7"N	2600–2000 BC	-16.5	5.3	Chen <i>et al.</i> (2014)
8	Shimao	110°19'31"E, 38°34'20"N	2200–1800 BC	-15.9	7.3	Cai (2015)

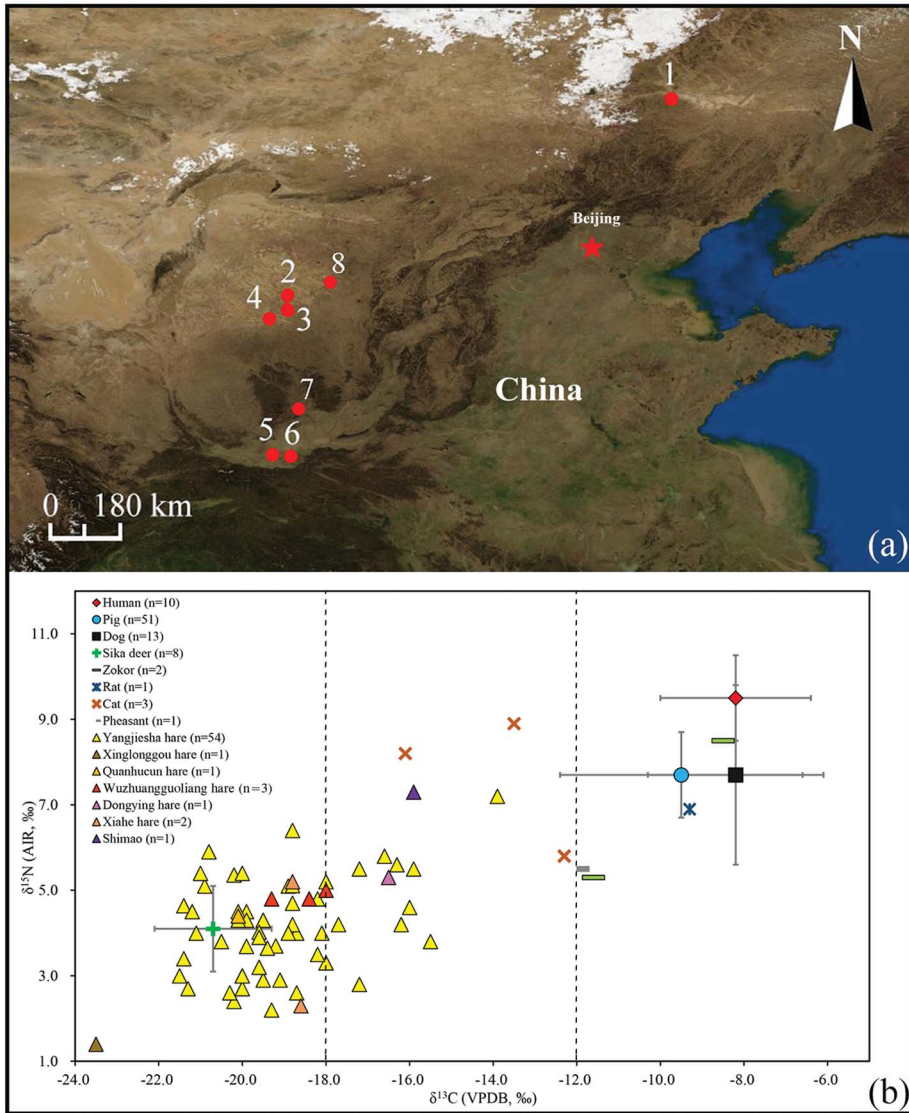


Figure 5. a) Map showing other sites near Yangjiesha; b) scatter plot of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of small-sized animals and mean \pm SD $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of humans, domesticates and wild animals recovered from these sites: 1) Xinglonggou; 2) Wangyangpan; 3) Yangjiesha; 4) Wuzhuangguoliang; 5) Dongying; 6) Qianhucun; 7) Xiahe; 8) Shimao. For additional information and references, see Tables 2–3 (figure by P. Sheng).

consumption. These hares probably lived next to or inside these ancient settlements, developing a commensal relationship with humans. People may even have encouraged or managed this relationship. This scenario appears likely for specimen 16Y33, which has the most ^{13}C -

(−13.9‰) and ^{15}N -enriched (7.2‰) values (Figure 6). A clear outlier compared to the other hares, this individual is close to the domestic pigs at Yangjiesha plotted on Figure 5. We suggest that 16Y33 may have been kept within a domestic setting sometime between *c.* 2900 and 2700 BC, although further morphometric evidence is required to support this claim.

We argue that, while the changes in hare isotopic values were predominately driven by the expansion of a millet-dominated agriculture on the Loess Plateau, climate change should also be considered as a potential influence on the changing isotopic values. Located at the northern limit of the East Asian summer monsoon, the Loess Plateau is particularly sensitive to fluctuations in the strength of this phenomenon. As the climate becomes drier and the monsoon weakens on the Loess Plateau, vegetation in the area shifts towards C_4 plants (e.g. Yang *et al.* 2015). Such vegetation, for example, increased by approximately 15 per cent in this area from the Last Glacial Maximum (*c.* 19 000 BP) to the Mid to Late Holocene (*c.* 4000 BP) (Yang *et al.* 2015). The period in question here, *c.* 5000–4000 BP, was one of known climatic instability (Yang *et al.* 2015), which could have driven large-scale changes in local vegetation. The increasingly C_4 -dominated isotopic signature of the hares in this region may thus also be indicative of climate change.

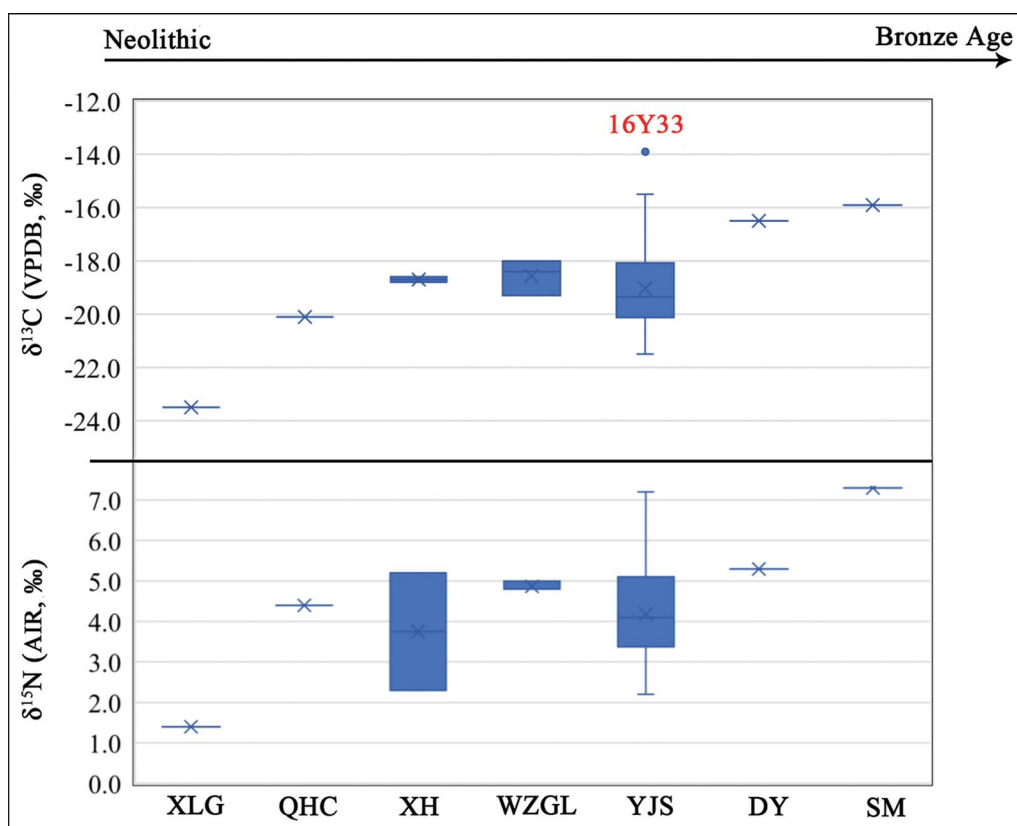


Figure 6. Box plots of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of hares from Neolithic to Bronze Age archaeological sites in northern China: XLG) Xinglonggou; QHC) Quanhuacun; XH) Xiahe; WZGL) Wuzhuangguoliang; YJS) Yangjiesha; DY) Dongying; SM) Shimao. For additional information and references, see Table 3 (figure by P. Sheng).

Ultimately, the changes in the isotopic values of Neolithic and Bronze Age hares on the Loess Plateau strongly suggest that extensive millet agriculture was a driving factor in the development of co-evolutionary interactions between humans and animals. While the specific consequences of this process remain unclear, this study clarifies the increasingly varied interactions of hares with ancient human settlements and cultivated fields. We recommend that more research be undertaken to establish baseline isotopic values for each sub-region of the Loess Plateau, in order to determine the relative influence of climate change and agricultural activities on the isotopic values of the local fauna.

Conclusion

Our study of early commensalism in hares in northern China, beginning *c.* 4900 years ago, shows that the isotopic signals from desert hare bones from the Late Neolithic site of Yangjiesha indicate that a sizeable proportion of hares consumed more millet or millet-based foods over time. As millet-based agricultural systems expanded throughout the Loess Plateau, desert hares and humans developed a commensal relationship, much like other animal species associated with the increasingly abundant crop plants in and around Neolithic settlements. The presence of commensal hares at Yangjiesha, and at the nearby sites of Dongying and Shimao, reveals changing human-hare interactions in northern China dating to *c.* 4900–3800 BP. These findings suggest that changing land-use patterns indirectly affected the diet and behaviour of small wild mammals on the Loess Plateau during the Mid to Late Holocene, a process that may have shaped co-evolutionary trajectories. Such a process, documented here from isotopic signatures in the Neolithic, is not only indicative of the spread of agriculture but also extends back in time the significance of human relationships with hares in China, where a range of archaeological, textual and iconographic data from the Bronze Age onwards show a varied and sustained relationship between humans and leporids.

Acknowledgements

This study was supported by grants from the National Natural Science Foundation of China (41471167); the National Social Science Fund of China (18ZDA218); a China Postdoctoral Science Foundation Grant (2018M641902); the National Natural Science Foundation of China Research Fund for International Young Scientists (41550110224); and the Chinese Academy of Sciences International Visiting Scholar Fellowship (2016VBC002). We also thank Yumeng Qu in Renmin University for the line drawing, and Michael Storozum for his useful comments and text revision.

Supplementary material

To view supplementary material for this article, please visit <https://doi.org/10.15184/aqy.2020.36>

References

- AMBROSE, S.H. 1990. Preparation and characterization of bone and tooth collagen for stable carbon and nitrogen isotope analysis. *Journal of Archaeological Science* 17:

- 430–51.
[https://doi.org/10.1016/0305-4403\(90\)90007-R](https://doi.org/10.1016/0305-4403(90)90007-R)
- AURA, J.E., J. JORDÁ, J.V. MORALES, M. PÉREZ, M.P. VILLALBA & J.H. ALCOVER. 2009. Economic transition in finis terra: the Western Mediterranean of Iberia, 15–7 ka BP. *Before Farming* 2: 255–65.
<https://doi.org/10.3828/bfarm.2009.2.4>
- BAO, Y.G., X.Y. ZHOU, H.B. LIU, S.M. HU, K.L. ZHAO, P. ATAHAN, J. DODSON & X.Q. LI. 2018. Evolution of prehistoric dryland agriculture in the arid and semi-arid transition zone in northern China. *PLoS ONE* 13: e0198750.
<https://doi.org/10.1371/journal.pone.0198750>
- BARTOSIEWICZ, L., Z.E. KOVÁCS & B. FARKAS. 2013. Pass the skeleton key: animals in an Early Copper Age inhumation burial from Pusztataskony–Ledence I, Hungary, in E. Starnini (ed.) *Unconformist archaeology: papers in honour of Paolo Biagi*: 77–88. Oxford: Archaeopress.
- BRONK RAMSEY, C. 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51: 337–60.
<https://doi.org/10.1017/S0033822200033865>
- BROWN, T.A., D.E. NELSON, J.S. VOGEL & J.R. SOUTHON. 1988. Improved collagen extraction by modified Longin method. *Radiocarbon* 30: 171–77.
<https://doi.org/10.1017/S0033822200044118>
- CAI, J.W. 2015. Study of radiocarbon dating and diet at the Shimao site, Shaanxi Province. Unpublished MA dissertation, Peking University, Beijing (in Chinese).
- CHEN, X.L., S.M. HU, Y.W. HU, W.L. WANG, Y.Y. MA, P. LÜ & C.S. WANG. 2014. Raising practices of Neolithic livestock evidenced by stable isotope analysis in the Wei River Valley, north China. *International Journal of Osteoarchaeology* 26: 42–52.
<https://doi.org/10.1002/oa.2393>
- DE NIRO, M. 1985. Post-mortem preservation of alteration of *in vivo* bone collagen isotope ratios in relation to paleodietary reconstruction. *Nature* 317: 806–809.
<https://doi.org/10.1038/317806a0>
- DONG, G.H., S.J. ZHANG, Y.S. YANG, J.H. CHEN & F.H. CHEN. 2016. Agricultural intensification and its impact on environment during the Neolithic in northern China. *Chinese Science Bulletin* 61: 2913–25 (in Chinese).
<https://doi.org/10.1360/N972016-00547>
- FULLER, D.Q. & C.J. STEVENS. 2017. Open for competition: domesticates, parasitic domesticoids and the agricultural niche. *Archaeology International* 20: 110–21.
<https://doi.org/10.5334/ai-359>
- GU, F. 2005. *The complete collection of unearthed jades in China: volume 14*. Beijing: Science Press (in Chinese).
- GUAN, L., Y.W. HU, S.M. HU, Z.Y. SUN, Y. QIN & C.S. WANG. 2008. Stable isotopic analysis on animal bones from the Wuzhuanguoliang site, Jingbian, northern Shaanxi. *Quaternary Sciences* 6: 1160–65.
- HOCKETT, B.S. & J.A. HAWS. 2002. Taphonomic and methodological perspectives of leporid hunting during the Upper Paleolithic of the Western Mediterranean Basin. *Journal of Archaeological Method and Theory* 9: 269–302.
<https://doi.org/10.1023/A:1019503030246>
- HU, S.M., Z.Y. SUN, L.P. YANG, N.W. KANG, M.M. YANG & X.Q. LI. 2013. Research on faunal remains from the Yangjiesha site in Hengshan County, Shaanxi Province. *Acta Anthropologica Sinica* 32: 77–92 (in Chinese).
- HU, Y. 2018. Thirty-four years of stable isotopic analyses of ancient skeletons in China: an overview, progress and prospects. *Archaeometry* 60: 144–56.
<https://doi.org/10.1111/arcm.12367>
- HU, Y.W., S.M. HU, W.L. WANG, X.H. WU, F.B. MARSHALL, X.L. CHEN, L.L. HOU & C.S. WANG. 2014. Earliest evidence for commensal processes of cat domestication. *Proceedings of the National Academy of Sciences of the USA* 111: 116–20.
<https://doi.org/10.1073/pnas.1311439110>
- The Institute of Archaeology, CASS. 1982. *The jades from Yinxu*. Beijing: Cultural Relics Press (in Chinese).
- 2003. *Oracle bone found at Huanyuandongdi, Yinxu site*. Kunming: Yunnan People’s Publishing House (in Chinese).
- JAANG, L., Z.Y. SUN, J. SHAO & M. LI. 2018. When peripheries were centres: a preliminary study of the Shimao-centred polity in the loess highland, China. *Antiquity* 92: 1008–22.
<https://doi.org/10.15184/aqy.2018.31>
- LEE-THORP, J.A. 2008. On isotopes and old bones. *Archaeometry* 50: 925–50.
<https://doi.org/10.1111/j.1475-4754.2008.00441.x>

- LEGG, B.J. 1876. *The she king, or the book of ancient poetry*. London: Trübner.
- LI, G.L. & J.Q. WANG. 2001. *Ancient fine arts in Shaanxi Han relief in Suide*. Xi'an: Shanxi People's Fine Arts Publishing House (in Chinese).
- LIU, L., X. ZHOU, Y. YU & Z. GUO. 2011. Soil organic carbon isotopic evidence of natural vegetation in the Loess Plateau. *Quaternary Sciences* 31: 506–13 (in Chinese).
- LIU, X.Y., M.K. JONES, Z. ZHAO, G. LIU & T.C. O'CONNELL. 2012. The earliest evidence of millet as a staple crop: new light on Neolithic foodways in north China. *American Journal of Physical Anthropology* 149: 283–90.
<https://doi.org/10.1002/ajpa.22127>
- LLOVERAS, L., J. MAROTO, J. SOLER, R. THOMAS, M. MORENO-GARCÍA, J. NADAL & N. SOLER. 2016. The role of small prey in human subsistence strategies from early Upper Palaeolithic sites in Iberia: the rabbits from the Evolved Aurignacian level of Arbreda Cave. *Journal of Quaternary Science* 31: 458–71. <https://doi.org/10.1002/jqs.2869>
- MANNERMAA, K. 2008. Birds and burials at Ajvide (Gotland, Sweden) and Zvejnieki (Latvia) about 8000–3900 BP. *Journal of Anthropological Archaeology* 27: 201–25.
<https://doi.org/10.1016/j.jaa.2008.01.001>
- REIMER, P.J. *et al.* 2013. Selection and treatment of data for radiocarbon calibration: an update to the International Calibration (IntCal) criteria. *Radiocarbon* 55: 1923–45.
https://doi.org/10.2458/azu_js_rc.55.16955
- RICHARDS, M.P. & R.E.M. HEDGES. 1999. Stable isotope evidence for similarities in the types of marine foods used by Late Mesolithic humans at sites along the Atlantic Coast of Europe. *Journal of Archaeological Science* 26: 717–22.
<https://doi.org/10.1006/jasc.1998.0387>
- Shaanxi Institute of Archaeology Research. 2009. *Bronzes from northern Shaanxi: volume IV*. Chengdu: Bashu Publishing House (in Chinese).
- SHENG, P.F., X. SHANG, Z.Y. SUN, L.P. YANG, X.N. GUO & M.K. JONES. 2018. North-south patterning of millet agriculture on the Loess Plateau: Late Neolithic adaptations to water stress, NW China. *The Holocene* 28: 1554–63.
<https://doi.org/10.1177/0959683618782610>
- SOMERVILLE, A.D., N. SUGIYAMA, L.R. MANZANILLA & M.J. SCHOENINGER. 2017. Leporid management and specialized food production at Teotihuacan: stable isotope data from cottontail and jackrabbit bone collagen. *Archaeological and Anthropological Sciences* 9: 83–97.
<https://doi.org/10.1007/s12520-016-0420-2>
- SZPAK, P., J.Z. METCALFE & R.A. MACDONALD. 2017. Best practices for calibrating and reporting stable isotope measurements in archaeology. *Journal of Archaeological Science: Reports* 13: 609–16.
<https://doi.org/10.1016/j.jasrep.2017.05.007>
- TURCOTTE, M.M., H. ARAKI, D.S. KARP, K. POVEDA & S.R. WHITEHEAD. 2017. The ecoevolutionary impacts of domestication and agricultural practices on wild species. *Philosophical Transactions of the Royal Society B* 372: 20160033.
<https://doi.org/10.1098/rstb.2016.0033>
- WANG, T.T., D. WEI, X. CHANG, Z.Y. YU, X.Y. ZHANG, C.S. WANG, Y.W. HU & B.T. FULLER. 2017. Tianshanbeilu and the Isotopic Millet Road: reviewing the Late Neolithic/Bronze Age radiation of human millet consumption from north China to Europe. *National Science Review* 6: 1024–39.
<https://doi.org/10.1093/nsr/nwx015>
- WANG, X., B.T. FULLER, P. ZHANG, S. HU & X. SHANG. 2018. Millet manuring as a driving force for the Late Neolithic agricultural expansion of north China. *Scientific Reports* 8: 5552.
<https://doi.org/10.1038/s41598-018-23315-4>
- WEISSBROD, L., F.B. MARSHALL, F.R. VALLA, H. KHALAILY, G. BAROZ, J.C. AUFRAY, J.D. VIGNE & T. CUUCHI. 2017. Origins of house mice in ecological niches created by settled hunter-gatherers in the Levant 15 000 y ago. *Proceedings of the National Academy of Sciences of the USA* 114: 4099–104.
<https://doi.org/10.1073/pnas.1619137114>
- WU, X.Z. & N.I. DROZDOV. 2016. Research on small mammals in zooarchaeology. *Acta Anthropologica Sinica* 35: 418–30 (in Chinese).
- YANG, S.L., Z.L. DING, Y.Y. LI, X. WANG, W.Y. JIANG & X.F. HUANG. 2015. Warming-induced north-westward migration of the East Asian monsoon rain belt from the Last Glacial Maximum to the Mid-Holocene. *Proceedings of the National Academy of Sciences of*

the USA 112: 13178–83.

<https://doi.org/10.1073/pnas.1504688112>

ZHANG, S.Q., Y. ZHANG, J.S. LI & X. GAO. 2016. The broad-spectrum adaptations of hominins in the later period of Late Pleistocene of China: perspectives from the zooarchaeological studies. *Science China Earth Sciences* 59:

1529–39.

<https://doi.org/10.1007/s11430-016-5287-7>

ZHAO, Z.J. 2011. New archaeobotanic data for the study of the origins of agriculture in China. *Current Anthropology* 52: 295–306.
<https://doi.org/10.1086/659308>