

<https://doi.org/10.1038/s40494-026-02455-1>

Acquisition and use of animal resources during the Longshan period in the northern Guanzhong region of China

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During the Longshan period (ca. 4350–3950 BP), the introduction of cattle, sheep, and goats transformed animal resource use across northern China. While the Northern Shaanxi Plateau adopted these domesticates early, fostering pastoralism, the southern Guanzhong region maintained the agricultural system established during the Yangshao period. The transitional zone between these regions, however, remains poorly understood. Analysis of animal remains from the Xiaweiluo site in central Shaanxi reveals that pigs were the primary domesticate, with wild species providing supplementary meat. The integration of cattle, sheep, and goats into the subsistence economy occurred later in Guanzhong than on the Northern Shaanxi Plateau. These findings highlight adaptive strategies in this transitional zone and offer new insights into how environmental factors and cultural choices shaped regional socio-economic systems in late Neolithic northern China.

Longshan (ca. 4350–3950 BP) represents a pivotal transitional period in Chinese prehistory, marked by increasing social complexity, technological innovation, and intensified regional interactions^{1,2}. During this period, while some regions experienced decline, others, particularly the middle Yellow River valley, saw settlement expansion, the emergence of proto-urban centers, and the consolidation of hierarchical social structures^{3–6}. As such, the Longshan period provides key insights into the early development of complex societies and the economic foundations that underpinned the rise of early Chinese civilization.

The Guanzhong region, located between the Northern Shaanxi Plateau and the Qinling Mountains, holds a key geographic and ecological position in early China. The Guanzhong region comprises two parts – Southern Guanzhong and Northern Guanzhong – each characterized by distinct landforms. The southern part consists of plains formed by the Wei River and its tributaries, while the northern part features loess tablelands (known as *yuan*)⁷. In terms of subsistence strategies, the Northern Shaanxi Plateau combined crop cultivation with early pastoralism, while Southern Guanzhong developed a mixed agricultural system dominated by rice, wheat, and millets, with livestock management playing a secondary role to crop farming^{8–11}. In contrast, Northern Guanzhong, situated between these two zones, remains relatively understudied. Archaeological and chronological

evidence indicates that domestic cattle, sheep, and goats entered China via the Eurasian steppe and oasis corridors, spreading southwards through Northern Guanzhong before reaching the southern plains^{12,13}. This underscores the role of Northern Guanzhong as a transitional corridor and highlights the importance of investigating animal resource acquisition and use in Northern Guanzhong for understanding the spread of domestic livestock, regional dietary strategies, and economic adaptations during the Longshan period.

The Xiaweiluo site, a large and well-preserved Longshan-period settlement in Northern Guanzhong, offers a unique opportunity to address these issues (Fig. 1). Earlier zooarchaeological research at the site focused primarily on species identification and quantification. However, recent advances in zooarchaeology enable a more detailed investigation into herd composition, age profiles, and the use of domestic and wild animals¹⁴.

This study investigates patterns of animal resource acquisition and use in Northern Guanzhong through a reanalysis of the animal assemblage recovered from Xiaweiluo, in comparison with data from the Northern Shaanxi Plateau and Southern Guanzhong. Specifically, this study examines how domestic pigs, cattle, sheep, and goats were incorporated into local subsistence strategies, and evaluates the role of Northern Guanzhong as a transitional corridor in the southward dispersal of domesticated animals.

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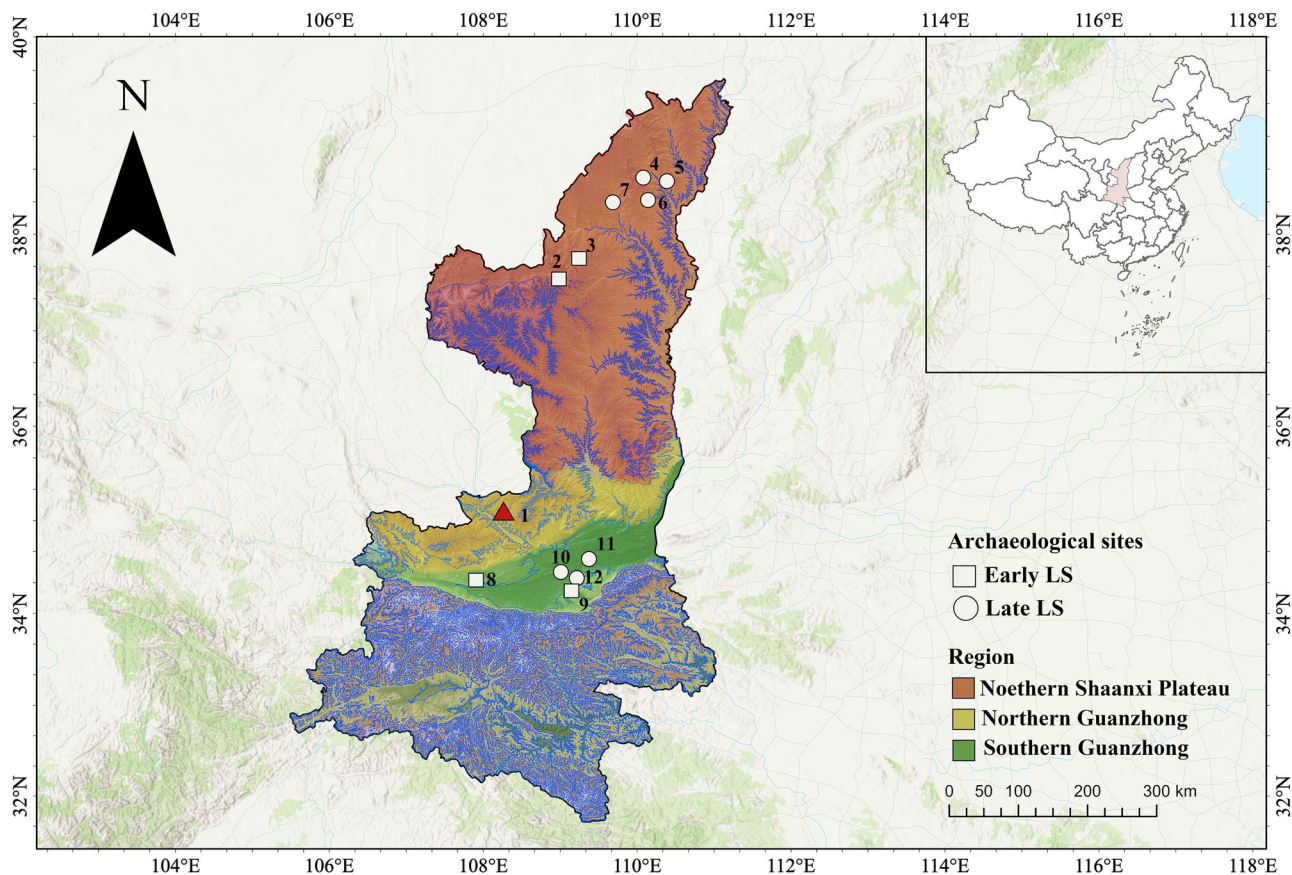


Fig. 1 | Map showing the location of archaeological sites mentioned in this study. LS denotes the Longshan period. Red, yellow, and green areas represent the Northern Shaanxi Plateau, Northern Guanzhong, and Southern Guanzhong, respectively; blue lines are contour lines. Red triangle marks the site of Xiaweiluo;

white squares and circles indicate Early and Late Longshan archaeological sites, respectively. Sites: 1. Xiaweiluo; 2. Miaoliang; 3. Jiadamao; 4. Muzhuzhuliang; 5. Shimao; 6. Zhaimaoliang; 7. Huoshiliang; 8. Anban; 9. Xinjie; 10. Dongying; 11. Kangjia; 12. Jiangzhai.

This study also reconstructs subsistence strategies in relation to local environmental conditions and settlement patterns. These findings provide new insights into the economic organization of Northern Guanzhong during the Longshan period and highlight how transitional zones shaped regional adaptations, contributing to the broader mosaic of early Chinese civilization.

Methods

The site of Xiaweiluo and the animal remains

Xiaweiluo is located in the northern part of the Guanzhong region, situated on a loess tableland adjacent to the Sanshui River, a tributary of the Jing River. The site lies on relatively elevated terrain with a gentle slope descending from northeast to southwest. In 2004, the School of Cultural Heritage at Northwest University, the Shaanxi Academy of Archaeology, and the Xunyi Museum jointly excavated the site. The excavation revealed an area of 1405 square meters and recovered various features, including houses, pits, burials, kilns, and ditches. The site has a long chronological sequence, spanning from the Neolithic Yangshao period through the Han Dynasty (Table 1). Cultural remains from the Longshan period are the most abundant and diverse, with all houses, most kilns and ditches, most pits, and one burial attributed to this period. The excavations recovered a wide range of artefacts, including pottery, stone tools, bone tools, and human and animal remains. Based on ceramic typology, the Longshan-period deposits were divided into early and late phases (known as Early Longshan and Late Longshan).

Animal remains were recovered from 17 archaeological features dating to Early Longshan and 25 feature dating to Late Longshan. The Early Longshan features include 2 houses, 14 pits, and 1 kiln, while the Late Longshan features comprise 5 houses, 19 pits, and 1 ditch¹⁴.

Table 1 | Chronological scheme associated with this study

Period	Date
Yangshao	ca. 7000 - 5000 BP
Longshan	ca. 4350 - 3950 BP
Zhou	ca. 2996 - 2206 BP
Qin	ca. 2171 - 2157 BP
Han	ca. 2152 - 1730 BP

Zooarchaeological analysis

The animal remains were numbered according to their excavation units. Each specimen was identified to taxon, skeletal element and part, side (left or right), stage of epiphyseal fusion, and dental eruption and wear. Information on traces of human modifications, preservation conditions, and other relevant taphonomic effects was also recorded.

Taxonomic identifications were made based on atlases¹⁵ and both modern and archaeological reference skeletal specimens housed in the Zooarchaeology Laboratory of the School of Cultural Heritage, Northwest University. For inclusion in NISP (Number of Identified Specimens) counts, specimens were required to be identified to at least the family level for mammals and to the class level for non-mammals.

Skeletal measurements were taken following the guidelines in *A Guide to the Measurement of Animal Bones from Archaeological Sites*¹⁶ and recorded in millimetres (mm). Dental wear of pigs was recorded following Grant¹⁷ and age estimation was based on the criteria established by Li¹⁸ for

domestic pigs from the Bronze Age YinXu site. Weathering stages was recorded according to Behrensmeyer¹⁹.

Ancient DNA analysis

Given the difficulties in morphologically distinguishing between cattle/water buffalo and sheep/goat, we conducted ancient DNA analysis on three specimens initially identified as the genus *Bos* and *Ovis/Capra* to ensure accurate species identification, including One caprine calcaneus from Early Longshan pit H20, one bovine talus from Late Longshan pit H65, and one caprine metatarsal from Late Longshan pit H21. Ancient DNA processing was performed in dedicated ancient DNA facilities at Peking University, following standard practices to minimize contamination. Bone samples were extracted using a silica-based protocol²⁰, with a modification of 5% bleaching (10 min) and UV irradiation (15 min per side) before digestion. Single-stranded libraries were built using the Santa Cruz Reaction (SCR) method²¹. The libraries were then amplified and dual-indexed following established protocols²², purified with AMPure XP beads, and sequenced on an Illumina Novaseq 6000 platform at Novogene Co. (Beijing, China) to generate 150 bp paired-end reads.

We analysed sequencing data using the nf-core/eager pipeline (v2.4.4)^{23,24} with default parameters plus "--mergedonly" to filter long-

fragment reads. Samples zooarchaeologically identified as cattle were mapped to *Bos taurus* (NCBI: GCF_002263795.3) and *Bubalus bubalis* (NCBI: GCF_003121395.1_ASM312139v1) genomes, while those identified as sheep were aligned to the domestic sheep genome (*Ovis aries*, NCBI: GCF_000298735.2). We mapped XBCO001 to the domestic sheep reference genome (GCF_016772045.2) and found a low endogenous molecule content (0.11%), and a terminal C to T rate of 8.4% (less than 10%), raising concerns about its authenticity of ancient data. Mitochondrial DNA mapping to the reference genomes of domestic sheep (NC_001941.1) and goat (NC_005044.2) yielded only 2% and 1.5% coverage, respectively. Overall, the poor preservation and limited data preclude reliable downstream analyses or confident species identification.

Sequencing reads were also mapped and realigned to mitochondrial reference genomes (*Bos taurus*: NC_006853.1; *Ovis aries*: NC_001941.1) using BWA-alm²⁵ and Circular Mapper (v1.93.5)²⁶, followed by duplicates removal (DeDup v0.12.8)²⁶ and quality filtering (SAMtools²⁷, MAPQ ≥ 30). Consensus sequences were generated with Schmutzi (v1.5.6)²⁸ and sequencing depth was calculated using SAMtools.

The sequences were aligned with modern reference sequences using MUSCLE (v5.1)²⁹. Maximum-likelihood phylogenetic trees were constructed with IQ-TREE2 (v2.3.6)³⁰ employing 1000 bootstrap replicates and visualized using iTOL (v6.9.1)³¹.



Fig. 2 | Animal remains from Longshan period contexts at Xiaweiluo. 1. Pig, occipital bone; 2. Sika deer, occipital bone; 3. Pig, mandible; 4. Sika deer, mandible; 5. Dog, mandible; 6. Sika deer, atlas; 7. Pig, ulna; 8. Dog, humerus; 9. Pig, pelvis; 10. Sika deer, pelvis; 11. Red deer, femur; 12. Sika deer, tibia; 13. Sika deer, talus; 14. Cattle,

talus; 15. Sheep, metapodial; 16. Sheep/goat, calcaneus; 17. Hare, mandibles, vertebrae, ribs, and limb bones; 18. Bamboo mouse, pelvis, femur, and tibia; 19. Tiger, metapodial; 20. Dog, baculum; 21. Phasianidae, accessory metatarsals; 22. Lamellibranchia, shell.

Table 2 | NISP and MNI of animal remains from Longshan period contexts at Xiaweiluo

Category	Taxon	Early Longshan				Late Longshan			
		NISP	NISP(%)	MNI	MNI(%)	NISP	NISP(%)	MNI	MNI(%)
Domestic mammals									
Artiodactyla	Cattle, <i>Bos taurus</i>	0	0.00	0	0.00	1	0.29	1	3.57
	Pig, <i>Sus domesticus</i>	155	34.22	17	43.59	209	59.89	12	42.86
	Sheep/goat, <i>Ovis aries/Capra hircus</i>	0	0.00	0	0.00	3	0.86	1	3.57
Carnivora	Dog, <i>Canis familiaris</i>	85	18.76	2	5.13	12	3.44	1	3.57
Total domestic mammals		240	52.98	19	48.72	225	64.47	15	53.57
Wild mammals									
Artiodactyla	Red deer, <i>Cervus elaphus</i>	2	0.44	1	2.56	1	0.29	1	3.57
	Roe deer, <i>Capreolus capreolus</i>	3	0.66	1	2.56	4	1.15	1	3.57
	Sika deer, <i>Cervus nippon</i>	42	9.27	3	7.69	34	9.74	2	7.14
	Large cervid	11	2.43	1	2.56	6	1.72	1	3.57
	Middle cervid	38	8.39	1	2.56	24	6.88	1	3.57
	Small cervid	4	0.88	1	2.56	23	6.59	1	3.57
	Unidentified cervid	11	2.43	1	2.56	0	0.00	0	0.00
	Caprid/Antelope, <i>Caprinae/Antilopinae</i>	2	0.44	1	2.56	0	0.00	0	0.00
Carnivora	Tiger, <i>Panthera tigris</i>	1	0.22	1	2.56	0	0.00	0	0.00
Lagomorpha	Hare, <i>Lepus</i>	74	16.34	3	7.69	10	2.87	1	3.57
Rodentia	Chinese bamboo rat, <i>Rhizomys sinensis</i>	9	1.99	1	2.56	0	0.00	0	0.00
	Unidentified species	9	1.99	1	2.56	6	1.72	1	3.57
Total wild mammals		206	45.47	16	41.03	108	30.95	9	32.14
Birds									
Galliformes	Unidentified phasianid	2	0.44	1	2.56	5	1.43	1	3.57
	Medium bird	2	0.44	1	2.56	4	1.15	1	3.57
Fishes									
Osteichthyes	Unidentified species	1	0.22	1	2.56	0	0.00	0	0.00
Molluscs									
Unionidae	Unidentified species	0	0.00	0	0.00	7	2.01	2	7.14
Reptiles									
Testudines	Unidentified species	2	0.44	1	2.56	0	0.00	0	0.00
Total wild non-mammals		7	1.55	4	10.26	16	4.58	4	14.29
Total		453	100.00	39	100.00	349	100.00	28	100.00

Results

A total of 1578 animal specimens were recovered from Longshan period contexts at Xiaweiluo. Among these, 392 specimens (24.84% of the assemblage) exhibited no signs of weathering (grade 0), while the majority - 950 specimens (60.20%) - showed slight to moderate weathering (grade 1-2). A smaller portion, 236 specimens (14.96%), were classified as grade 3. Traces of gnawing or chewing by rodents and carnivores were observed on 187 specimens (11.85%), and 60 specimens (3.80%) showed traces of burning. In addition, a total of 45 specimens (2.85%) displayed anthropogenic modifications, including cut marks, striations, or grinding.

The animal remains from Longshan period contexts yielded 802 taxonomically identifiable specimens, including 453 specimens from Early Longshan contexts and 349 from Late Longshan contexts. The MNI (Minimum Number of Individuals) per phase was 39 (Early Longshan) and 28 (Late Longshan), respectively. Notably, ZooMS (Zooarchaeology by Mass-spectrometry) analysis of a large carnivore metacarpal bone revealed that this specimen belonged to a tiger. (Fig. 2, Table 2).

Pig (*Sus scrofa domesticus*)

The size of the mandibular third molar (M3) is a key criterion for distinguishing domestic pig from wild boar^{32,33}. We compared the M3 measurements

of pigs from Xiaweiluo with those of domestic pigs from the Neolithic sites of Jiangzhai and Longshangang, as well as with modern wild boar specimens collected from the Wangwu Mountain³⁴⁻³⁶. The results indicate that the pigs from Xiaweiluo can be identified as domestic, as their M3 measurements closely align with those of domestic pigs from Longshangang (Fig. 3).

A total of 49 pig mandibles were recovered from the site, of which 34 could be aged based on dental eruption and wear. Among these, 21 specimens date to the Early Longshan and 13 to Late Longshan (Fig. 4). The age-at-death Mortality profiles indicate that Early Longshan pigs cluster into three age groups: 5–8 months, 9–14 months, and 18–24 months. In contrast, the mortality during Late Longshan is more heavily concentrated within the 18–24-month range.

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The age-at-death profile is a useful indicator for understanding the aims of pig husbandry and patterns of meat consumption in ancient

communities. Pigs slaughtered at 1.5–2 years of age were typically raised for meat, as this age range yields the highest return on investment^{18,37}. Assemblages dominated by young pigs generally suggest household-level

production and consumption, while those with few young individuals often reflect herds raised primarily for exchange rather than local use³⁸. Urban sites tend to show more uniform mortality profiles, whereas rural sites display greater variability³⁹. Modern wild boar mate in October and farrow in April or May⁴⁰. Assuming that domestic pigs in antiquity followed a similar reproductive cycle, it is possible to reconstruct the likely slaughter season at Xiaweiluo.

At Xiaweiluo, pig mortality during the Longshan period spans a broad range, with very few individuals surviving into adulthood. For the early and late phases, pigs slaughtered before two years of age make up about 95% and 85% of the respective assemblages. Early Longshan pigs were slaughtered primarily between the autumn–winter of their birth year through the following spring, with another peak in the subsequent autumn–winter. In contrast, Late Longshan slaughter was concentrated in the autumn–winter period following the year of birth. Together, these patterns reflect a rural subsistence strategy centred on local husbandry and local consumption, in which pigs were raised primarily as a source of meat for the community itself.

Dog (*Canis familiaris*)

A total of 97 canid specimens were identified, representing a minimum of three individuals. Of these, 85 identifiable dog specimens were recovered from Early Longshan contexts, accounting for 18.81% of all identifiable faunal remains from that phase. These specimens represent a minimum of two individuals (8.11% of the total MNI). Notably, one nearly complete skeleton came from pit H77. In contrast, Late Longshan contexts yielded 12 identifiable dog specimens, representing 3.44% of

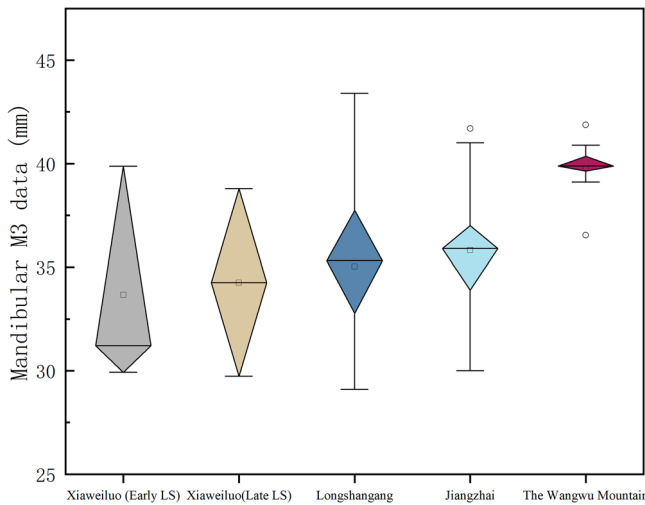


Fig. 3 | Comparison of mandibular M3 measurements among pig populations. Each column represents the distribution of mandibular M3 lengths in pigs from each site; diamonds indicate the interquartile range (IQR), with the horizontal line inside representing the median; circles indicate outliers; squares indicate the mean value.

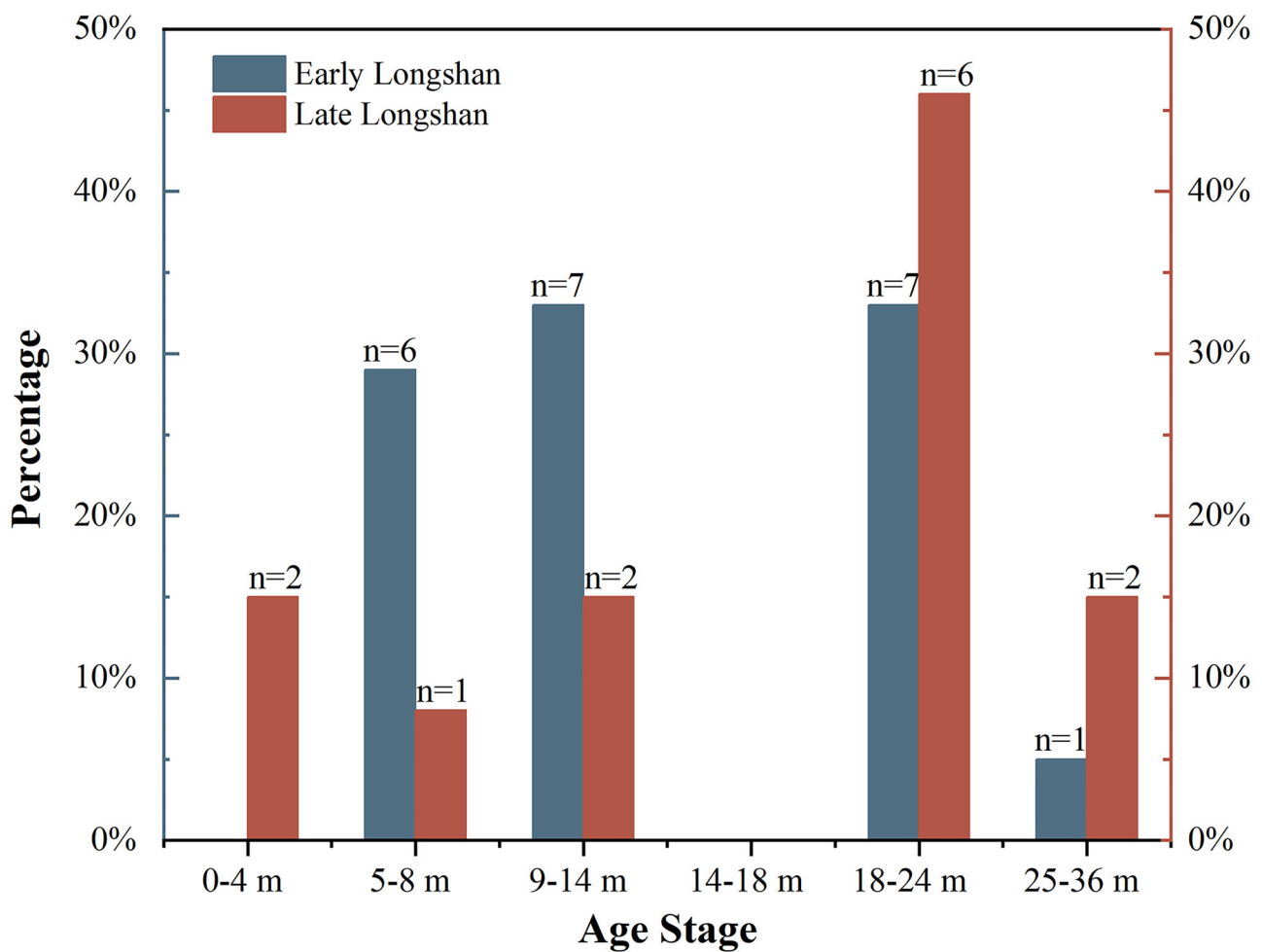


Fig. 4 | Age-at-death profile of domestic pigs from the Longshan period contexts at Xiaweiluo. Columns represent the percentage of domestic pigs in each age group among individuals with identifiable age; blue and red indicate Early and Late Longshan data, respectively.

Table 3 | Comparison of measurement data taken from mandibles of canids from Xiaweiluo, dogs from Huoshiliang, and a modern female wolf (unit: mm)

Measurements	Xiaweiluo		Huoshiliang	Modern Female Wolf
	Early LS	Late LS		
Slot length of P ₁ -P ₄	34.00	32.26	35.40–37.30 (n = 3)	51.4
Slot length of M ₁ -M ₃	33.72		31.30–33.80 (n = 3)	47.56
Slot length of P ₁ -M ₃	62.58		66.20–70.40 (n = 2)	96.16
Slot length of M ₁	19.36	18.93	19.00–20.20 (n = 2)	28.67
Mandibular height between P ₃ and P ₄	17.59	18.99	18.10–21.28 (n = 2)	25.61
Mandibular thickness between P ₃ and P ₄	9.45	8.86	9.10–11.00 (n = 3)	12.68

LS Longshan.

Table 4 | Comparative metrics of cattle bones from the Longshan period contexts at Xiaweiluo and cattle/water buffalo remains from Dongying site (unit: mm)

Measurement items	Xiaweiluo (Late LS)	Dongying (LS)	
		Cattle	Water buffalo
Maximum length of inner half (GLm)	61.95	58.8	79.80
Maximum thickness of inner half (Dm)	37.89	35.6	50.1
Maximum length of outer half (GLI)	66.48	66.2	90.7
Maximum thickness of outer half (DI)	37.53	37.4	46.9

LS Longshan.

identifiable remains from that phase and a minimum of one individual (3.70% of the total MNI).

The morphology and size of the mandible are standard criteria for distinguishing dogs from wild canids. In this study, two mandibles from Early Longshan contexts and one from Late Longshan contexts were recovered, none of which retained teeth. All three mandibles show a curved ventral margin of the horizontal ramus, a characteristic feature of domestic dogs⁴¹. Metric data from these specimens were compared with dog assemblages from the Longshan period site of Huoshiliang in northern Shaanxi⁴², and with a modern adult female wolf specimen housed at the Zooarchaeology Laboratory of the School of Cultural Heritage, Northwest University. Linear metrics -including mandible length and the length of the M1 alveolus- from Xiaweiluo fall largely within or below the ranges documented for dogs. Moreover, the Xiaweiluo mandibles are markedly smaller than those of the modern adult female wolf. Taken together, the morphological and metric evidence support the identification of the canid remains from Xiaweiluo as dogs (Table 3).

Cattle (*Bos taurus*)

Only one large bovine specimen -a talus from Late Longshan context- was unearthed at Xiaweiluo, accounting for 0.29% of the NISP and 3.57% of the MNI.

Compared with cattle and water buffalo reference bones housed in the Zooarchaeology Laboratory at Northwest University, the large bovine talus from Xiaweiluo lacks the small medial projection that extends beyond the anterior margin on the inner side, and its posterior projection on the lateral side rises only slightly above the highest point of the anterior margin. These characteristics are more consistent with cattle than with water buffalo. In terms of the size, the large bovine talus from Xiaweiluo is smaller than all water buffalo specimens from the Longshan period site of Dongying in Gaoling, Shaanxi Province⁴³ and falls within the size range of cattle from that assemblage.

In addition, cattle remains have been identified at other Longshan period sites in Northern Guanzhong. For instance, at the Nantou Locale of the Xitou site, also in Xunyi County, 19 cattle specimens were recovered, accounting for 8.4% of the total NISP and representing a minimum of one

individual (3.6% of the total MNI)⁴⁴. It is important to note that mitochondrial DNA (mtDNA) analysis confirmed that the large bovine talus from Xiaweiluo belongs to domestic cattle (*Bos taurus*) (see Table S1). Radiocarbon dating of this specimen yielded an age of 3730 ± 30 BP, with a calibrated date of 4153–3981 cal. BP. Taken together, the morphological characteristics, metric comparisons, and genetic evidence establish the large bovine cattle specimen from Xiaweiluo as domestic cattle (Table 4, Fig. 5, Fig. 6).

Sheep/goat (*Ovis aries*/*Capra hircus*)

A total of three sheep/goat specimens were recovered from Late Longshan contexts at Xiaweiluo, representing a minimum of one individual. These specimens account for 0.87% of the total NISP and 3.75% of the total MNI.

The caprine specimens from Xiaweiluo are metrically consistent with domestic caprines from the Bronze Age Erlitou site in Yanshi, Henan Province⁴⁵, supporting their identification as domesticated taxa. Mitochondrial DNA analysis of a metatarsal from Late Longshan context confirmed it as sheep of haplogroup B (Table S1). Radiocarbon dating of this specimen yielded an age of 3700 ± 30 BP, with a calibrated range of 4098–3967 cal. BP (Table 5; Fig. 6, Fig. 7).

Zooarchaeological data from Xiaweiluo demonstrate that domestic animals, primarily pigs, constituted the primary source of meat throughout the Longshan period in Northern Guanzhong. Cattle and sheep were incorporated only in the late phase and in limited numbers, while wild resources continued to be exploited consistently as a supplementary component. This pattern reflects a flexible subsistence strategy and confirms the persistence of a traditional pig-based economy in Northern Guanzhong during the Longshan period.

Discussion

At Xiaweiluo, domestic animals accounted for approximately 53.42% of the total NISP during the early Longshan period, while increasing to about 64.47% in the late Longshan period. The MNI values for domestic animals remained relatively stable across both phases. These data suggest that domestic animals were the primary source of meat for the inhabitants of Xiaweiluo throughout the Longshan period. (Fig. 8).

Tree scale: 0.01

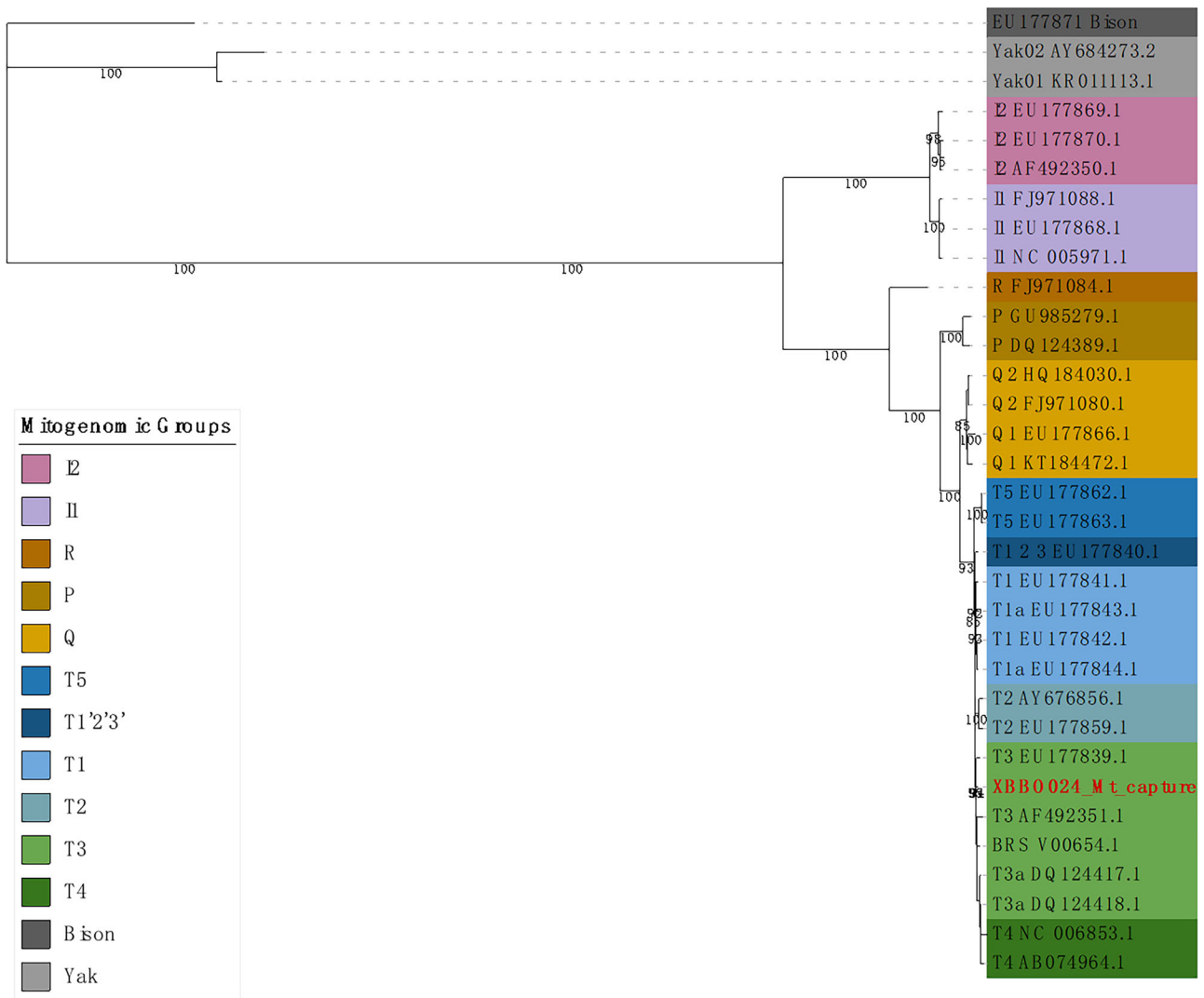


Fig. 5 | Rooted maximum likelihood tree of Bos species based on mitochondrial genomes.

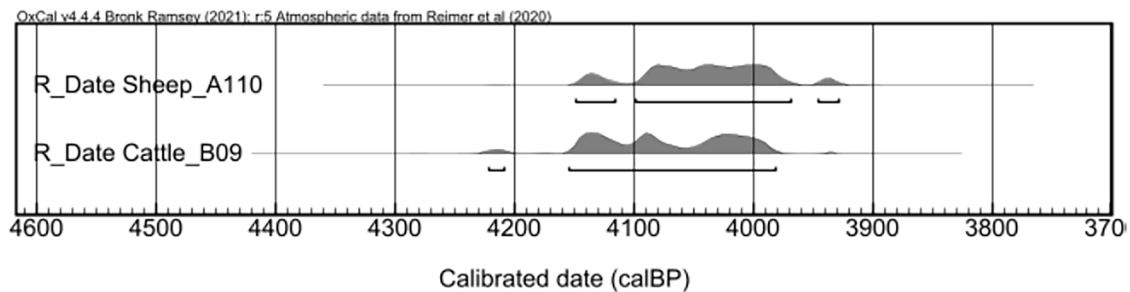


Fig. 6 | Radiocarbon dating results of animal bones from Xiaweiluo. The calibration of the dates was conducted in OxCal v4.4.4 using Int Cal 20 as the calibration curve^{80,81}. Used 95.4% probability calibrated ranges.

Notably, a marked shift occurs in the relative proportions of dogs and pigs over time. From Early Longshan to Late Longshan, the NISP proportion of dogs decreased from 35% to 5%, while pigs increased from 63% to 92%. A similar trend is evident in the MNI values. Cattle and sheep/goats appeared only in Late Longshan, each comprising 1% of the NISP and 7% of the MNI. (Fig. 9).

To better understand patterns of animal-resource acquisition and use in Northern Guanzhong during the Longshan period, we compared the Xiaweiluo assemblage with data from eleven sites on the Northern Shaanxi Plateau and in Southern Guanzhong. As the MNI values are unavailable for several of these sites, the analysis relied exclusively on NISP data (Table 6).

For most early Longshan period sites on the Northern Shaanxi Plateau, as well as in Northern and Southern Guanzhong, domestic animals dominate faunal assemblages, accounting for over 60% of the

identified specimens. Miaoliang is a notable exception, where domestic animals represent only 19% of the assemblage. In the late Longshan period, the proportion of domestic animals surged across the region,

Table 5 | Comparative metrics of Longshan period sheep bones from Xiaweiluo and sheep remains from the Bronze Age site of Erlitou (unit: mm)

Skeletal element	Measurement items	Xiaweiluo		Erlitou (Phase I-IV)
		Early LS	Late LS	
Metatarsal	Distal (maximum) width (Bd)		25.29	21.15 ~ 28.34(n = 17)
	Distal (minimum) thickness Dd		11.11	14.01 ~ 19.03(n = 17)
Teeth	Second molar length		18.59	12.50 ~ 20.20 (n = 53)
	Second molar width		7.99	7.88 ~ 10.55 (n = 54)

Tree scale: 0.01

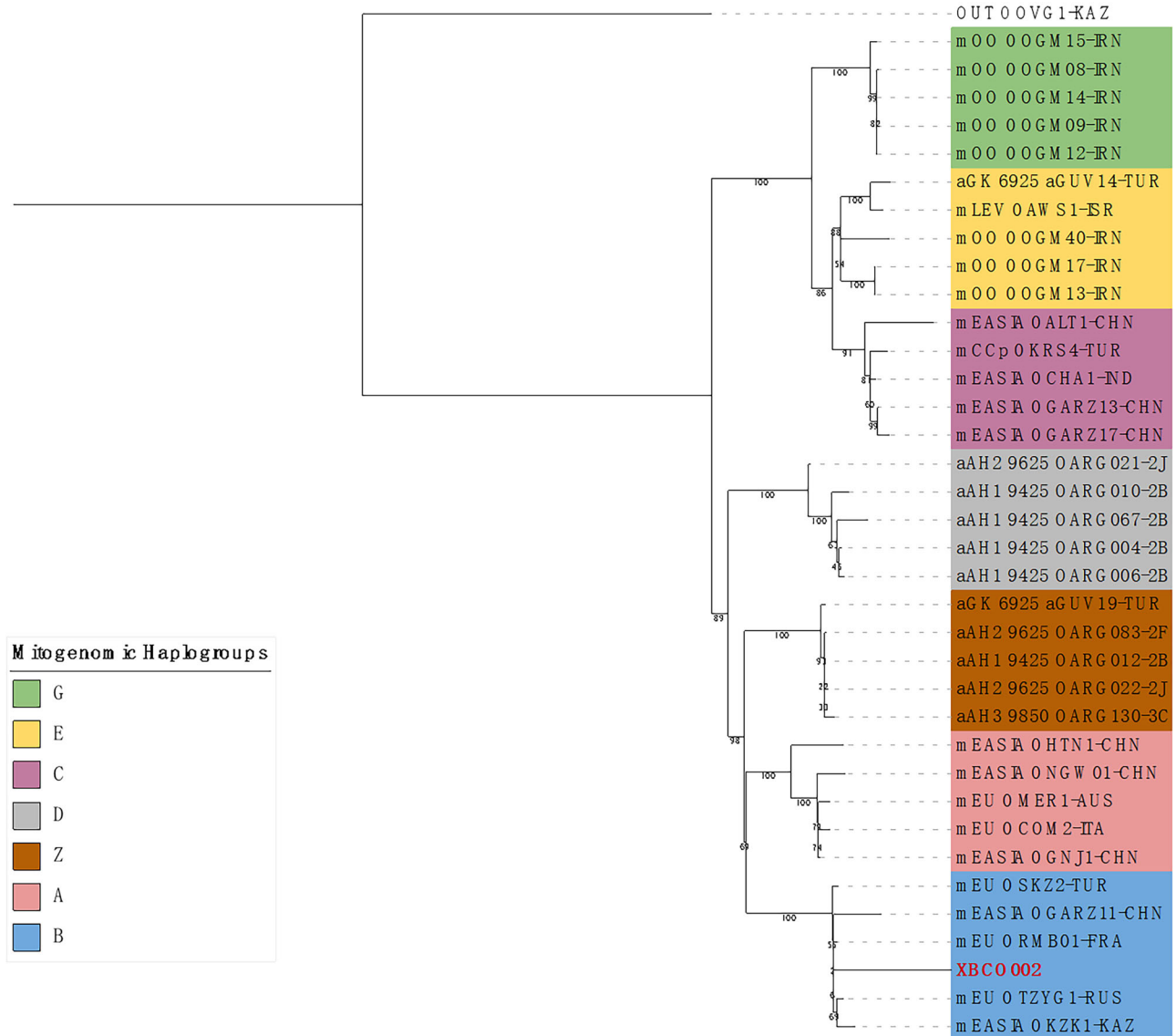


Fig. 7 | Rooted maximum likelihood tree of Ovis species based on mitochondrial genomes.

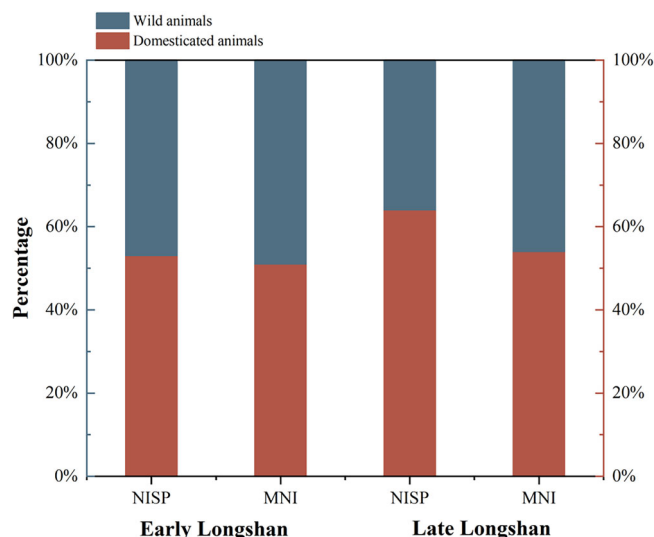


Fig. 8 | The NISP and MNI ratios of domesticated and wild animals from the Longshan period contexts at Xiaweiluo.

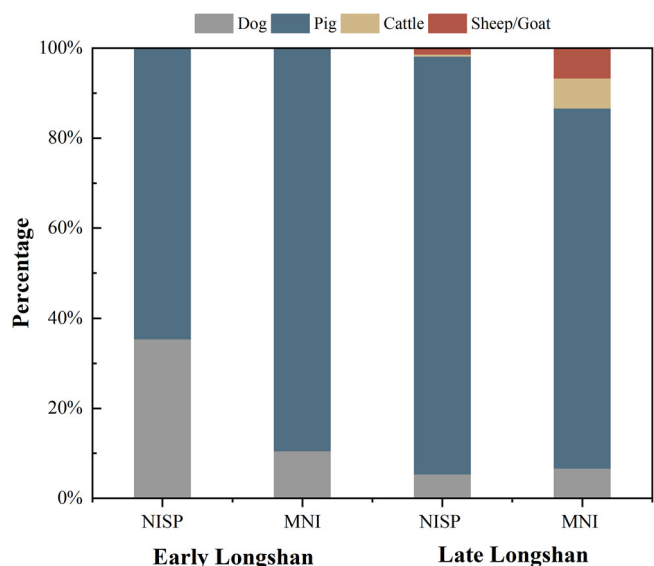


Fig. 9 | The proportions of NISP and MNI of domesticated animals during the Longshan period at Xiaweiluo.

exceeding 90% at all sites on the Northern Shaanxi Plateau. In Northern Guanzhong, the frequency of domestic animals increased by approximately ten percent at Xiaweiluo. In contrast, all three sites in Southern Guanzhong saw a decline.

Among the domesticates, cattle and caprines constitute a significant portion of the assemblages at sites on the Northern Shaanxi Plateau, and at Miaoliang. They outnumber pigs. This pattern stands in sharp contrast to early Longshan period sites in both Southern Guanzhong and Northern Guanzhong, where cattle and caprines are absent. In the late Longshan period, the composition of domesticates also shifted: the proportion of cattle and sheep/goats on the Northern Shaanxi plateau increased considerably, surpassing pigs to become the predominant domesticated animals. During the same period, cattle and sheep/goats also appeared in Southern and Northern Guanzhong, with a higher proportion of these taxa in Southern Guanzhong than in Northern Guanzhong. As summarized in Table 6, these patterns illustrate a diverse and complex landscape of animal resource exploitation across Shannxi.

Previous research indicates that domestic cattle, sheep, and goats entered China via the Eurasian steppe and oasis corridors between 5500 and 4500 cal. BP, subsequently spreading rapidly across the upper and middle reaches of the Yellow River^{46–49}. Situated adjacent to the Mongolian Plateau, the Northern Shaanxi Plateau functioned as a key corridor for the southward dispersal of these animals⁵⁰. Direct evidence from the Northern Shaanxi Plateau supports this timeline: two cattle bones from the Hongliang site date to 4406–4186 cal. BP and 4405–4158 cal. BP, respectively, and sheep bones from both Hongliang and Miaoliang also date to the same period^{50,51}. Radiocarbon data from the Xiaweiluo further confirm that cattle and sheep/goats appeared later in Northern Guanzhong. To date, no definitive radiocarbon data for cattle and sheep/goats have been obtained from Southern Guanzhong. Therefore, it remains unclear whether cattle and sheep/goats reached Southern Guanzhong via Northern Guanzhong or through an alternative route.

As noted in previous studies, the distinctive geographical and environmental conditions of the Northern Shaanxi Plateau facilitated the rapid adoption of cattle and sheep/goats as primary sources of meat, laying the foundation for one of the earliest pastoral economies in China⁵². The characteristic landforms of the Northern Shaanxi Plateau, including tablelands (*yuan*), ridges (*liang*), and gullies (*mao*), provided grazing areas that did not compete with arable land. While unsuitable for millet cultivation, these gullies and ravines were ideal for pasture. This interpretation is supported by stable carbon and nitrogen isotope analysis, which indicates that sheep and goats in this region foraged in open, natural environments^{53–55}. Archaeobotanical evidence further confirms the presence of wild fodder plants during the Longshan period, such as shrub lespedeza (*Lespedeza bicolor*), Japanese clover (*Kummerowia striata*), and sweet yellow clover (*Melilotus officinalis*)^{56,57}. In addition, the biological traits of sheep and goats—their small body size, drought tolerance, and rapid reproduction—made them particularly well-adapted to the arid conditions of the Northern Shaanxi Plateau^{58,59}.

Compared to the Northern Shaanxi Plateau, Southern Guanzhong features a flatter topography, with the Wei River and its tributaries providing abundant water resources. This setting was well suited to the development of early dry farming agriculture, while rivers and woodland also offered habitats for wild animals. As a result, from Early Longshan to Late Longshan, wild animals consistently formed part of the animal resources exploited by communities in Southern Guanzhong. The proportion of wild animals was closely related to site size. Medium- and large-sized sites, such as Anban⁶⁰ and Xinjie⁶¹, covered larger areas, implying larger resident populations. Local wild resources were likely insufficient to meet the dietary needs of these communities. Consequently, larger sites relied more heavily on the husbandry of domestic animals to ensure a stable meat supply. (Table 7).

The tablelands of Northern Guanzhong, in contrast to the deeply dissected and fragmented landscape of the Northern Shaanxi Plateau, feature relatively intact and extensive surfaces that are more suitable for agricultural development. Although no precise data on the area of Xiaweiluo are available, the excavators consider it to be a large settlement. This suggests that, like the large sites in Southern Guanzhong, Xiaweiluo likely relied on domestic animal husbandry to meet the meat demands of its resident population.

During Early Longshan, the composition of domestic animals was similar in both Southern and Northern Guanzhong, with pigs being the primary domestic species in both zones. During Late Longshan, however, the introduction of cattle and sheep/goats prompted the emergence of divergent animal exploitation strategies between these two zones. This structural difference was likely the result of climatic change, in conjunction with shifts in human-environment interactions.

Around 4000 BP, a cooling event occurred^{62,63}. Some scholars suggest that this climatic shift may have disrupted the balance between population and resources^{64,65}. Settlement archaeology reveals that during the Longshan period, site density in Northern Guanzhong was relatively low, with settlements distributed discontinuously. In contrast, Southern Guanzhong

Table 6 | Proportions of domestic animals across Longshan period sites on the Northern Shaanxi Plateau and in the Guanzhong region

Period	Zone	Site	Total NISP	NISP (%)				
				Domestic Mammals	Dog	Pig	Cattle	Sheep/Goat
Early LS	Northern Shaanxi Plateau	Jiadamao ⁵¹	439	67	9	85	1	4
		Miaoliang ⁵¹	227	19	0	14	60	26
	Southern Guanzhong	Anban (Phase III) ⁷³	1318	71	2	98	0	0
		Xinjie ⁷⁴	632	63	8	92	0	0
	Northern Guanzhong	Xiaweiluo	452	54	35	63	0	0
Late LS	Northern Shaanxi Plateau	Muzhuzhulian ⁷⁵	3014	92	9	24	24	43
		Shimao ⁷⁶	2767	94	2	29	21	48
		Zhaimaoliang ⁷⁶	399	95	1	26	39	34
		Huoshiliang ⁷⁷	1111	95	1	12	21	66
	Southern Guanzhong	Dongying ⁴³	502	57	7	54	32	7
		Kangjia ⁷⁸	419	33	12	55	33	
		Jiangzhai (Phase V) ³⁶	195	12	46	49	5	0
	Northern Guanzhong	Xiaweiluo	349	64	5	92	1	1
LS	Northern Guanzhong	Xitou ⁴⁴	227	88	5	79	10	7

LS Longshan.

Table 7 | The size and proportion of wild animals of Longshan-period archaeological sites in Southern Guanzhong

Zone	Period	Site	Size (m ²)	Proportion of wild animals (NISP)
Southern Guanzhong	Early Longshan	Anban (Phase III) ⁶⁰	above 700,000	21%
		Xinjie ⁶¹	c. 300,000	37%
	Late Longshan	Dongying ⁴³	Severely damaged remnant 9,000	43%
		Kangjia ⁷⁹	c. 190,000	67%
		Jiangzhai (Phase V) ³⁶	c. 20,000	88%
Northern Guanzhong	Early Longshan	Xiaweiluo ¹⁴	Large scale*	46%
	Late Longshan			36%

*The excavation reports do not provide data on the size of the site.

exhibited higher settlement density and more clustered distributions⁶⁶, indicating greater population pressure in the south. Archaeobotanical evidence further shows that from the Yangshao to the Longshan period, as rice farming expanded northwards, the proportion of millet in the agricultural system of Southern Guanzhong declined^{67,68}. Stable isotope data from Southern Guanzhong indicate that pigs consumed a diet based mainly on C₄ plants such as millet^{69,70}, whereas cattle, sheep, goats, and wild cervids relied primarily on C₃ wild plants. In response to reduced availability of millet and other C₄ resources, communities may have reduced pig husbandry, as pigs depended heavily on millet-based fodder^{71,72}. At the same time, they introduced cattle and sheep/goats, -animals capable of thriving on C₃ wild plants- to ensure a stable supply of meat.

Although there is currently no definitive evidence indicating changes in the agricultural structure of northern Guanzhong during the late Longshan period, the relatively low settlement density in this region suggests that population pressure was relatively moderate. The traditional approach to obtaining animal resources -primarily raising domestic pigs supplemented by hunting wild animals- was sufficient to meet the population's meat consumption needs. Consequently, the traditional reliance on pigs as the primary source of meat was maintained. Since pigs alone were able to meet dietary needs, there was likely little incentive to shift toward large-scale husbandry of cattle and sheep/goats. This partly explains the persistent pattern in Northern Guanzhong: cattle and sheep/goat were never raised on a large scale, as the existing subsistence system remained effective.

A comparative analysis across the Northern Shaanxi Plateau, Northern Guanzhong, and Southern Guanzhong reveals distinct regional trajectories in animal use. On the Northern Shaanxi Plateau, favourable environmental conditions supported the early adoption of cattle and sheep/goats as primary domesticates, contributing to the emergence of one of the earliest pastoral economies in China - although small-scale sites relying mainly on wild resources also existed. Northern Guanzhong, situated between these two zones, maintained a traditional pig-based husbandry system, reflecting its stable resource base and relatively low population density.

These findings highlight the complex interplay of environmental conditions, settlement patterns, and cultural choices in shaping regional animal husbandry strategies. The spread of animal domesticates in late Neolithic northern China was neither uniform nor linear; rather, it was characterised by regionally-specific adaptations. As illustrated by the case of Xiaweiluo, transitional zones such as Northern Guanzhong fostered distinct economic systems, in which traditional practice persisted alongside the selective incorporation of new species. This regional mosaic, reflecting both local ecological adaptations and broader interregional connections, was a fundamental feature of the socio-economic fabric of early Chinese civilization. By synthesizing zooarchaeological data with chronological, environmental, and settlement evidence, this study provides additional insights into human-animal interactions and socio-economic organization in late Neolithic northern China.

Data availability

All data are provided within the main text of the manuscript or the Supplementary Information. Mitochondrial genome sequences generated in this study have been deposited in GenBank, including a **Bos taurus** mitogenome (accession PX725379) and an **Ovis aries** mitogenome (accession PX725380).

Received: 12 June 2025; Accepted: 11 March 2026;
Published online: 07 April 2026

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Acknowledgements

The authors thanks to Mrs. Xintian Liu and Mrs. Yumeng Tian (School of Cultural Heritage, Northwest University) for their assistance in data collection. This study was supported by Major Project of the Ministry of Education of China: "Building an Independent Knowledge System of Chinese Archaeology" Sub-project: "The Development of the Origins of Chinese Civilization" (grant number 2024JZDZ055), National Social Science Fund of China (grant number 24XKG004), National Natural Science Foundation of China (grant number U2574205), The Archaeological Talent Promotion Program of China (grant number 2024-267). The authors would also like to acknowledge the editors and anonymous reviewers for their constructive feedback on this manuscript.

Author contributions

Y.L. and J.X. designed the research; R.G. and Z.H. analyzed animal remains, X.L., Y.H. and H.Y. performed ancient DNA analysis; R.C. produced maps and figures; H.C. conducted excavations and acquired funding; R.G. and Y.Q. wrote the original manuscript and contributed equally to this work; Y.L., J.X., and C.Z. reviewed and edited the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s40494-026-02455-1>.

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