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Sex in the city: Uncovering sex-specific management of equine resources from prehistoric times to the Modern Period in France

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ABSTRACT

Sex identification from fragmentary archeozoological assemblages is particularly challenging in the Equid family, including for horses, donkeys and their hybrids. This limitation has precluded in-depth investigations of sex-ratio variation in various temporal, geographic and social contexts. Recently, shallow DNA sequencing has offered an economical solution to equine sex determination, even in environments where DNA preservation conditions is not optimal. In this study, we applied state-of-the-art methods in ancient DNA-based equine sex determination to 897 osseous remains in order to assess whether equal proportions of males and females could be

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found in a range of archeological contexts in France. We found Magdalenian horse hunt not focused on isolated bachelors, and Upper Paleolithic habitats and natural traps equally balancing sex ratios. In contrast, Iron Age sacrificial rituals appeared to have been preferentially oriented to male horses and this practice extended into the Roman Period. During Antiquity, the Middle Ages and the Modern Period, cities emerged as environments largely dominated by horse males. This strong sex-bias was considerably reduced, and sometimes even absent, in various rural contexts. Combined with previous archaeozoological work and textual evidence, our results portray an urban economy fueled by adult, often old, males, and rural environments where females and subadults of both sexes were maintained to sustain production demands.

1. Introduction

Recent DNA work on equid archaeological remains from France has started to illuminate the temporal, cultural and sociological factors underlying horse (*Equus caballus*), donkey (*E. asinus*) and mule management during the last 2,500 years (Lepetz et al., 2021). This revealed that donkeys remained largely absent in the northern part of the country during the Iron Age, where they first appeared from the 1st century CE (Common Era) (Lepetz et al., 2021). While donkeys were present along the Mediterranean shores during the 5th century BCE (Before Common Era) (Columeau, 2000; Ugolini et al., 1991), they remained anecdotal in the northern part of the country during the whole Roman Period, which instead represented a Golden Age for mules. Donkeys superseded mules from the Merovingian Period (6th-8th centuries CE) and became increasingly important during the following Carolingian Period (8th-10th century CE) to represent almost one third of Medieval equine assemblages between the 11th and 13th centuries CE.

While based on an extensive dataset of 873 equine osseous remains, this first work (Lepetz et al., 2021) only provided a first, preliminary panorama as many time periods and/or geographic regions remain understudied. For example, the whole diversity of hunting strategies developed by Paleolithic hunter-gatherers is still undocumented at the DNA level, despite the technique potential to reveal whether specific horse family groups, sex and phenotypes were preferentially targeted (Bignon, 2006). The same holds true for our understanding of the selection criteria that guided animal sacrificial practices during Gallic and Roman Periods (Méniel, 2008; Lepetz and Van Andringa, 2008) but also, more generally, for those economic conditions that drove equine breeding decisions during history.

Various archaeozoological analyses informing on the past demographic structure of equine populations can contribute to fill this important gap in knowledge. For example, dental morphological patterns can reveal age class distributions (Levine, 1999), while the unexpected abundances of particular skeletal elements can unveil selective transportation of hunted carcasses from a kill site (Olsen, 2006; Bignon, 2008). Isotopic analyses can also help identify pastoral mobility and seasonality patterns (Bendrey et al., 2017; Albizuri et al., 2019; Lazzerini et al., 2020) while sex-ratios can shed light on whether male and female animals were considered evenly in hunting, breeding and ritual activities (Nistelberger et al., 2019; Fages et al., 2020). Sex determination in equids comes, however, with important limitations. Indeed, the presence of canines is generally considered diagnostic for males, but can exceptionally appear among adult females (Cornevin and Lesbre, 1894). The pelvis offers multiple morphological criteria for robust sex determination (Sisson, 1914; Barone, 1976) but remains less abundant than long bones in archaeological assemblages, for which no clear sexual dimorphism is present (Johnstone, 2004; Levine, 1979). Recently, next-generation DNA sequencing, especially X-to-autosomal (Schubert et al., 2017) or Y-to-autosomal (Nistelberger et al., 2019) alignment rates, has offered a solution to these problems by delivering robust sex identification as long as ~1,000 sequences can be aligned on the horse reference genome (Fages et al., 2020). The approach can, thus, be applied at relatively moderate costs to even specimens showing limited ancient DNA preservation, which holds potential to revisit models on the evolution of sex-ratio management in equids.

The current paradigm for France is mostly based on morphometric archaeological data, supporting Magdalenian hunting strategies focused on sex-balanced harem-like family groups rather than isolated bachelors (Bignon, 2006). Males are also known to have represented a preferential or even exclusive sacrificial resource during the Iron Age and the Roman Period, although age, and potentially coat coloration, mattered as well (Méniel and Lepetz, 2002; Scheid, 1998). This is well-established for sanctuaries or collective burials such as Vertault (Méniel and Jouin, 2000) and Le Cendre-Gondole (Foucras et al., 2019), respectively, in which complete skeletons could be excavated. However, most of the material available in other contexts has remained incompatible with sexual determination (Brunaux and Méniel, 1983; Méniel, 1992). A full characterization of the entire range of sacrificial practices at the time is, thus, still pending. Similarly, the material present in Gallic food wastes has helped depicting butchery activities evenly balanced between males and females, but preferentially oriented toward old animals (Méniel, 1994). The consumption of horse meat was, however, not widespread at the time, and was generally depreciated during the Roman Period, from the first century CE (Arbogast et al., 2002). For this reason, equine bones remain relatively rare in Roman domestic dumps. This appears in striking contrast to those assemblages excavated in the city outskirts, in which considerable amounts of equid carcasses could be evacuated and accumulated (Lepetz et al., 2013).

Equid material has also remained scarce and fragmentary during the Medieval and Modern Period. For instance, it represents only 0.7% (Rhone-Alpes region) to 2.1% (Languedoc) of the assemblages relative to cattle, sheep and pigs between the 6th and 16th century CE (Forest, 1997/98), despite being present in over two thirds of 140 archaeological sites (Rodet-Belarbi et al., 2017). In these conditions, only rendering deposits have delivered sufficient material for statistical comparisons, with a handful of sites portraying activities strongly biased towards old males (Parent-Duchâtelet, 1827; Arbogast et al., 2002; Barme and Clavel, 2015; Rodet-Belarbi et al., 2017).

Textual evidence has remained especially elusive regarding sex-specific horse husbandry techniques in early Medieval France. Grégoire de Tours's '*Historia Francorum*' reported that special care was paid to mares in large estates or rural domains, which hints at differentiated horse husbandry strategies between males and females at least from the 6th century CE (Bautier and Bautier, 1980). Strict legal rules governed livestock production, including for horses, and property at the time but the overall nature and quality of such production remains poorly documented, apart from abbey charters, where access to horse mounts was ruled (Bautier, 1981). Although horse husbandry was limited both in range and numbers (Fossier, 1968), textual sources provide important details on the composition of equine herds during the Carolingian Period (8th-10th century CE) (Prévot and Ribémont, 1994). For example, '*L'inventaire d'Annape*' reported that an average of one stallion every 20 mares was present in *villae* rural establishments, from the early 9th century CE. Outside abbeys, textual evidence remains, however, insufficient to characterize the broad range of horse production modes until the end of the Middle ages, when regional production, royal studs and trading sustained an increasing horse demand for transportation and war (Bautier and Bautier, 1980).

Overall, our current understanding of past management strategies of equine resources remains limited for France across space, time and

social contexts, especially regarding the respective roles of males and females. In this study, we used state-of-the-art approaches in ancient DNA research to complement the dataset generated by Lepetz et al. (2021) with 27 additional ancient horse remains from 6 Upper Paleolithic sites. We applied the Zonkey statistical package to shallow next-generation DNA sequence data in order to determine the sex of a total of 897 individuals. This represented 134 archaeological sites spanning the Upper Paleolithic (Upper Magdalenian and Azilian; N = 27 samples) and a time period extending from the Iron Age to the Modern Period (N = 870 samples). The Upper Paleolithic data provided a baseline for natural patterns of equine sex ratio and in relation to hunting, while the remaining material offered a first glimpse at the respective role of males and females in equine production, consumption and sacrifice.

2. Material and methods

2.1. Archaeological samples

A total of 897 equine remains were collected from 134 archaeological sites and subjected to the DNA analysis fully described by Lepetz et al. (2021) and following the same sequence quality, alignment and statistical requirements. The vast majority of the underlying sequence data was previously reported, in studies aimed at taxonomic identification (Gaunitz et al., 2018; Fages et al., 2019; Fages et al., 2020; Lepetz et al., 2021). Novel DNA sequence data were generated for the present study, representing a total of 25444516 sequence reads from 27 samples obtained from six Upper Paleolithic sites, all of which confirmed as horses (Fig. 1). These include four Magdalenian habitats from the Paris Basin (N = 9; Le Closeau, Étiolles, Tureau-des-Gardes, Grand-Canton and Pincevent; Table S1; Supplementary Information), one Azilian habitat (Le Closeau, N = 5) and one natural site from Southwestern France, at Igue du Gral, Sauliac-sur-Célé (N = 13). The latter site corresponds to a natural trap, which provides a baseline for assessing sex ratios in natural horse populations and testing for potential differences with habitat sites. Sex-ratio were determined using the Zonkey pipeline (Schubert et al., 2017), with default parameters, and applying the same filters as those from Fages and colleages (Fages et al., 2020). This proved sufficient for a total of 897 specimens, including the 27 novel specimens reported here and 870 (out of the 873) specimens presented by Lepetz et al. (2021). As described in Lepetz et al. (2021), sampling was originally focused on petrosal bones but was successfully extended to teeth and post-cranial skeletal elements, ensuring that individuals were sampled only once.

We strictly selected one type of bones only and restricted sampling from the same side of the animal for those sites showing large accumulations of bones. In the settlement sites (where non-equid animals were also accumulated), bones were preferentially collected from different structures across the excavation site. Whenever several bones were present within a given structure, individuals of different sizes and/or ages were collected. Samples were discarded in case no obvious differences could be observed.

Combined, our dataset consists of a majority of horses, representing a total of ~82.6% (741/897) of the samples analyzed, but also includes substantial fractions of donkeys (100/897 ~ 11.1%) and hybrids, with ~ 6.1% of mules (55/897) and only one single hinny (Table S1). The Iron Age and Roman Period are documented by a total of 127 (~14.1%) and 270 (~30.1%) remains, respectively. They represent a diversity of archaeological contexts, including rural habitats and ritual deposits (see

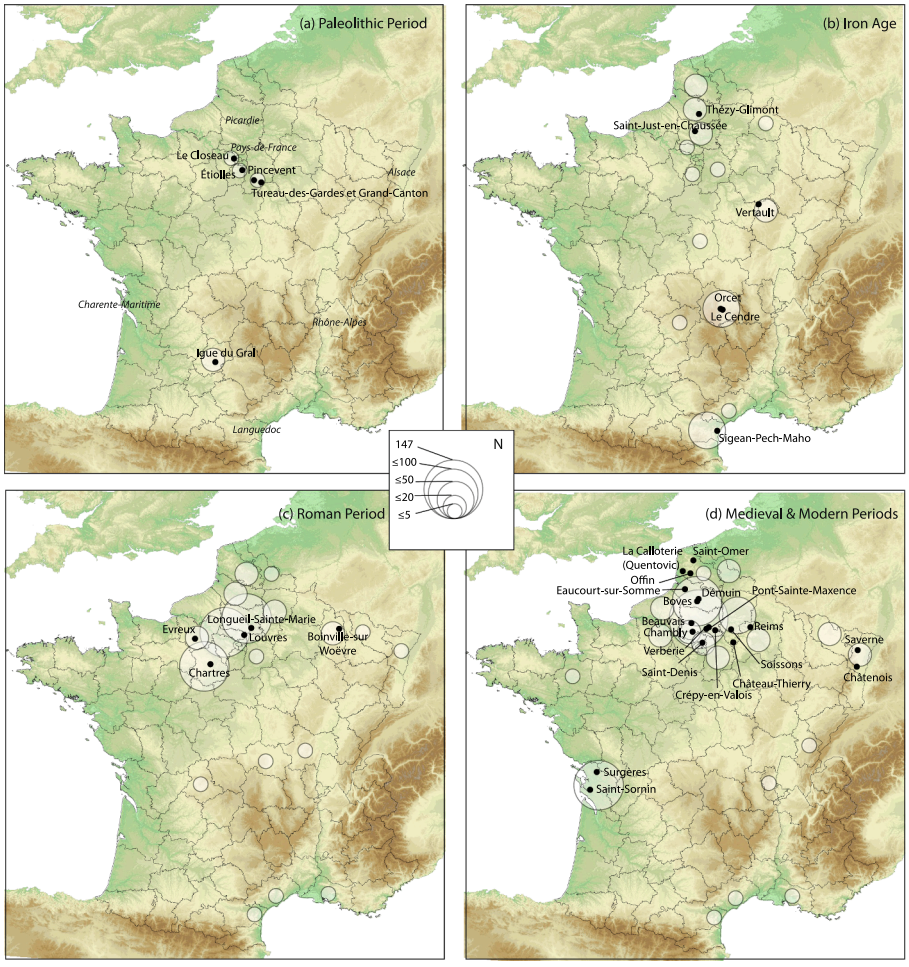

Fig. 1. Geographic location of the archaeological sites investigated in this study. Panel a: Paleolithic Period. Panel b: Iron Age (5th-1st century BCE). Panel c: Roman Period (1st-5th centuries CE). Panel d: Medieval & Modern Period (5th-18th centuries CE). The size of the circles is commensurate with the number of samples amenable to ancient DNA sequencing. Only the sites mentioned in this article are located on the map. The complete site projections are presented in Lepetz et al. 2021, Fig. 1.

Lepetz et al., 2021 for a full description and Supplementary Material 2). The Medieval material comprises a total of 444 remains (~49.5%), 436 of which allowing for robust social and cultural characterization.

The Medieval and Modern Period were subdivided into the four main time periods described below.

The first period spanned the 7th to 10th centuries CE and included a total of 113 samples, mostly from rural farms and villages ('*civil rural*' thereafter; 67/113 ~ 59.3%), castral sites (38/113 ~ 33.6%, including rural castles but also the Offin horse (excavated from an elite burial) and urban elites (8/133 ~ 7.1%). The Urban elite sites comprise remains from the Château-Thierry castle and the episcopal palace at Beauvais, but also the '*Rue Barrabin*' site at Surgères, which had strong connection with the city castle at the time (Vacher, 2018). This was also the case of the '*Vismaret*' site at La Calotterie, which was located in the ancient harbor of Quentovic, a city of rich merchands (Wood, 2006), thus, representing the '*urban elite*' category.

The second period extended from the 11th to 13th centuries CE and was represented by a total of 94 samples, mostly across '*civil rural*' (27/94 ~ 28.7%) and '*rural castle*' categories (42/94 ~ 44.7%). The remaining samples were obtained from urban contexts, including the three elite sites (21/94 ~ 22.3%) from the episcopal palace at Beauvais, the Saint Crépin Abbey at Soissons and the '*Rue Barrabin*' site at Surgères. They also included other urban sites reflecting more modest social contexts (4/94 ~ 4.2%), such as at Pont-Sainte-Maxence (14 Rue Bodchon), Saint-Omer (Rue Saint-Sépulcre) and Saint-Denis (Rue Charles Michel).

The late Middle Ages defined the third time period, with 81 samples dated to between the 14th and 16th centuries CE. These samples were distributed almost equally between '*civil rural*' contexts (villages: 21/81 ~ 25.9%), rural castles (24/81 ~ 29.6%) and rural monasteries (19/81 ~ 23.4%) as well as '*civil urban*' contexts (17/81 ~ 20.9%). It is noteworthy that the '*Rue Barrabin*' site at Surgères did belong to the latter category and not any longer to elite contexts at the time.

Finally, the last time period investigated corresponded to the Modern Period (16th to18th centuries CE) and was mainly marked by rural trading networks and important economic crises until the French Revolution in 1789. Approximately one fifth of the 148 remains belonging to this period (29/148 ~ 19.6%) came from '*civil rural*' contexts, represented both by villages (e.g. '*Impasse du Moulin*' at Chambly and '*La plaine d'Herneuse*' at Verberie) and castles such as at Saint-Sornin and Eaucourt-sur-Somme, which became agricultural establishments at the time. In the 17th century CE, the castle at Boves ('*Le Château*') was dismantled to become a stone quarry, and Châtenois was no longer belonging to elite categories. For convenience, they were classified as rural sites. Sites from '*civil urban*' contexts then provided the major fraction of samples (85/148 ~ 57.4%), while '*rural elite*' and '*urban non-monastic religious*' categories comprised the remaining 9 (~6.1%) and 25 (~16.9%) remains.

Chi-squared statistical tests were carried out in the R programming language while the factorial analysis was done in the PAST software (version 3).

3. Results

3.1. Upper Paleolithic sites

Our dataset combines a total of 27 Upper Paleolithic horse remains, including 12 males and 15 females. This provides evidence for balanced sex ratios in this time period (Chi-squared test, p-value = 0.5637), in line with earlier reports based on other Upper Paleolithic sites from across Belgium to Siberia (Fages et al., 2020). Interestingly, the presence of balanced sex-ratios is not statistically rejected when conditioning the analyses to those Magdalenian habitat sites (Chi-squared test, p-value = 1. 0) or the natural trap at Igue du Gral (Chi-squared test, p-value = 0.4054). This finding rules out horse prey hunting strategies focused significantly on one specific sex during the time period investigated in this sample.

3.2. Gallic sites

Considering all horse remains from archaeological sites belonging to the Hallstatt and La Tène A periods together suggested balanced sex ratios (4 *vs* 4), but the effective size is too limited to be meaningful. However, an over-representation of horse males was statistically supported when La Tène sites were considered altogether (103 *vs* 24; Chi-squared test, p-value = 2.381×10^{-12}). This signal was mainly driven by sacrificial sites (82 *vs* 15; Chi-squared test, p-value = 1.026×10^{-11}), as the sex-ratio was not as strongly unbalanced and the test was considerably less statistically significant when conditioning on habitat sites only (21 *vs* 9; Chi-squared test, p-value = 0.02846). The selection of males in sacrificial rituals was especially pronounced at Vertault (N = 9), Le Cendre (Gondole; N = 8) and Orcet (N = 36), where no females were identified (Chi-squared test, p-value = 3.335×10^{-13}). The bone assemblages were also sex-biased at Pech-Maho, despite the presence of females on site (18 *vs* 7; Chi-squared test, p-value = 0.02781). The over-representation of male horses was, however, not a universal rule, as balanced sex-ratios characterized the Saint-Just-en-Chaussée sanctuary (4 *vs* 6; Chi-squared test, p-value = 0.5271).

3.3. Gallo-Roman sites

The horse was no longer the only species identified in our dataset from the Roman Period (Lepetz et al., 2021) (Fig. 2). Regardless of the taxonomic group considered, sex-ratios were found to be biased towards males, as 157 horse males were identified for only 46 mares (Chi-squared test, p-value = 6.665×10^{-15}), 38 males for 14 females in mules (Chi-squared test, p-value = 8.741×10^{-4}) and 12 donkey jacks for 3 jennies (Chi-squared test, p-value = 0.0201). For donkeys, it is noteworthy that 11 of the 15 samples investigated came from a single site (Boinville-sur-Woëvre) and could, thus, reflect local patterns. Importantly, different sex-ratios were measured in different socio-cultural contexts (Fig. 3), with rural sites supporting generally balanced representations of males and females (12 *vs* 8, Chi-squared test, p-value = 0.3711). This was also true at the Zac du Parc site (Louvres), a dump site located near grouped settlements, no matter whether horses (17 *vs* 23, Chi-squared test, p-value = 0.3428) or mules (6 *vs* 5, Chi-squared test, p-value = 0.763) were considered. The situation was strikingly different for urban archaeological sites, which were dominated by males (117 *vs* 15 ~ 88.6%; Chi-squared test, p-value < 2.2×10^{-16}), both in horses (90 *vs* 10, Chi-squared test, p-value = 1.244×10^{-15}) and mules (27 *vs* 5, Chi-squared test, p-value = 1.006×10^{-4}).

Interestingly, the ritual site from Longueil-Sainte-Marie (L'Orméon, 2nd-3rd centuries CE) only delivered skulls and coxal bones that were extremely degraded, precluding sex identification based on morphological criteria. The molecular analyses carried out in this study revealed that only male horses were deposited (N = 26; Chi-squared test, p-value = 3.414×10^{-7}), suggesting horse sacrificial selection criteria similar to those observed during the Iron Age.

3.4. Middles Ages and the Modern Period

In contrast to previous periods, our dataset uncovered a whole range of situations during the Medieval and Modern time periods, with some sites over-representing horse males (e.g. '*Rue des Capucins*', '*Rue Hincmar*', and '*Rue Clovis*' at Reims (Barme and Clavel, 2021); 13 *vs* 3, Chi-squared test, p-value = 0.0124), and others showing balanced sex-ratios in both horses (e.g. '*Impasse du Moulin*' at Chambly, 11 *vs* 13; Chi-squared test, p-value = 0.6831) and donkeys (e.g. '*Rue Barrabin*' at Surgères, 8 *vs* 4: Chi-squared test, p-value = 0.2482, and; '*Tour de Broue*' at Saint-Sornin, 5 *vs* 5; Chi-squared test, p-value = 1.0). Considering all sites together, and disregarding social contexts, the first and the second Middle Ages appeared to over-represent horse males, with 60 *vs* 32 (Chi-

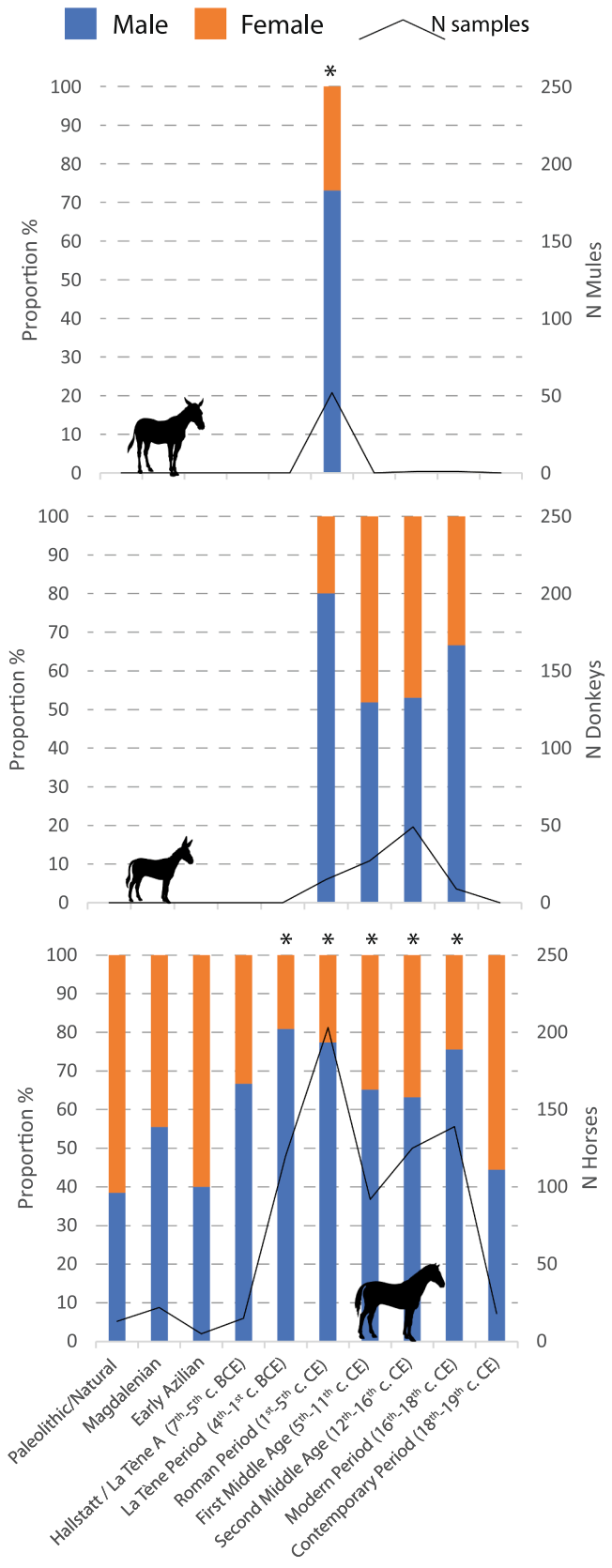

Fig. 2. Temporal changes of mule (top), donkey (middle) and horse (bottom) sex-ratios. Sex-ratios are provided as the proportion of males (blue) identified in each category. The proportion of females is shown in orange. The total numbers of remains included in the analysis are also reported. *: Statistical significance.

squared test, p-value $= 3.509 \times 10^{-3}$) and 79 *vs* 46 (Chi-squared test, p-value $= 3.161 \times 10^{-3}$) remains identified, respectively (Fig. 2). The situation was different for donkeys, which were characterized by balanced sex-ratios in both time periods (14 *vs* 13 and 26 *vs* 23; Chi-squared test, p-values $= 0.8474$ and 0.6682, respectively). However, both species were characterized by an increased over-representation of males during the following Modern Period (16th–18th centuries CE) (105 *vs* 34 for horses, and 6 *vs* 3 for donkeys; Chi-squared test, p-values $= 1.721 \times 10^{-9}$ and 0.3173, respectively), although the trend was not statistically significant for donkeys, where the effective size considered was limited.

Binning sites within time periods provides a simple manner to identify temporal trajectories. It does not, however, account for the whole social complexity possibly affecting equine resource management, nor for possible differences between rural and urban contexts. Yet, while both urban and rural sites showed an over-representation of horse males during the Medieval and Modern periods (113 *vs* 24 and 130 *vs* 84; Chi-squared test, p-value $= 2.876 \times 10^{-14}$ and 1.664×10^{-14}, respectively), confirming the overall temporal trend observed above, the proportion of mares was significantly larger in rural sites (Chi-squared test, p-value $= 2.849 \times 10^{-5}$). A similar increase in the female proportion was measured in donkeys, but it remained not significant (16 *vs* 7 and 32 *vs* 30 in cities and rural contexts, respectively; Chi-squared test, p-value $= 0.2161$). In fact, all rural contexts investigated in this study showed balanced sex-ratios in horses and donkeys during the medieval period (7th-16th centuries CE) (Chi-squared tests, $0.0811 \leq p\text{-values} \leq 1$), excepting rural castles for horses, where males were over-represented (53 *vs* 20, Chi-squared test, p-value $= 1.123 \times 10^{-4}$). Combined, our data set portrays a Medieval Period in which horse males were the most common equine resource in cities and rural castles, while donkeys and horses of both sexes were evenly represented in rural villages and monasteries. The same trends were observed for the Modern Period (Fig. 3); urban contexts: 88 *vs* 18, Chi-squared test, p-value $= 1.053 \times 10^{-11}$; rural contexts: 17 *vs* 16, Chi-squared test, p-value $= 0.8618$), except that none of these castles remained active then, and could, thus, be investigated.

A factorial analysis of the 436 samples belonging to the Medieval and Modern Periods recapitulated the strong difference observed between rural and urban contexts along the second factorial axis (Fig. 4). This difference was maintained throughout the four time periods considered (i.e. 7th-10th centuries CE, 11th-13th centuries CE, 14th-16th centuries CE, and; 16th-18th centuries CE). The first factorial axis mainly highlighted the changing preference to donkey jacks in civil/elite urban contexts during the 11th-13th centuries CE. It also revealed equine management strategies varying according to social contexts, with increasing proportions of horse mares and donkey jennies within rural monasteries and elite contexts, especially during the 14th to 18th centuries CE, although never significantly exceeding those of males.

4. Discussion

In this study, we applied shallow shotgun DNA sequencing and the Zonkey bioinformatic pipeline to identify the sex of 897 ancient equine remains excavated from 134 archaeological sites in France. Calculation of sex-ratio across sites, time periods and social contexts shed new light on the history of equine population management, especially regarding the preferential selection of males or females in various situations, including hunting, sacrificial rituals and husbandry.

4.1. Prehistoric hunting

Previous work on Late Glacial bone assemblages from the Paris Basin have highlighted the importance of horses for the subsistence economies of local hunter-gatherers (Bridault et al., 2003; Bignon, 2006; Bignon, 2008). Seasonality and paleo-demographic profiles have portrayed hunting episodes focused on family groups, including mares as well as

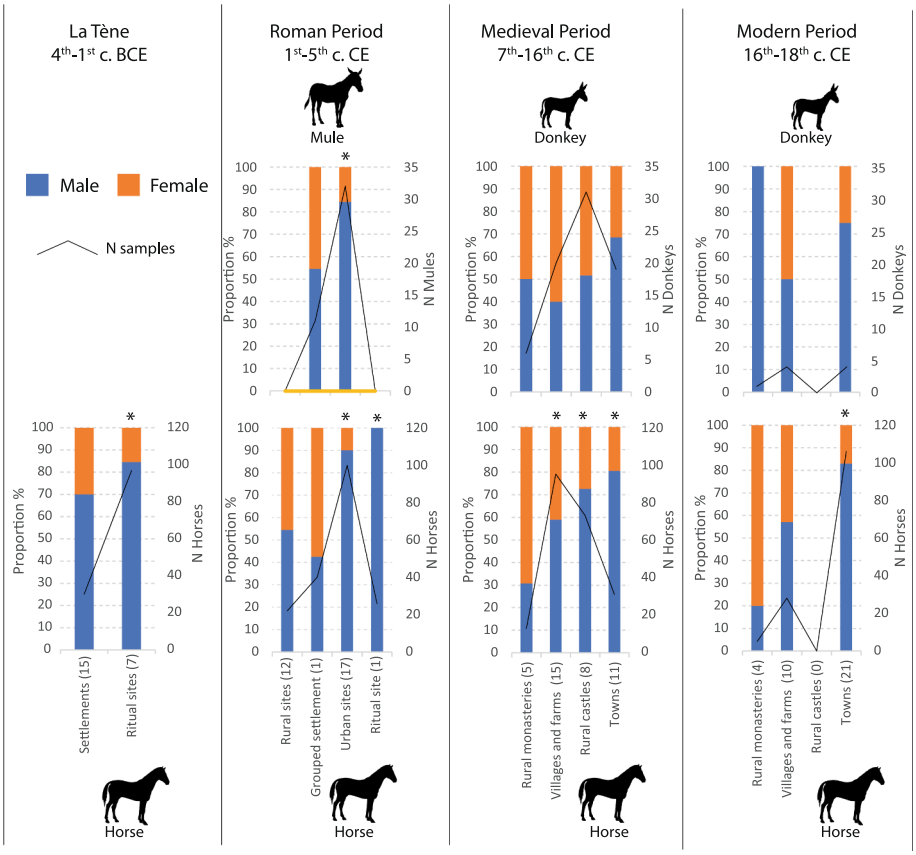

Fig. 3. Distribution of sex-ratio across cities and various rural contexts during the Iron Age (La Tène, 4th-1st centuries BCE), the Roman Period (1st-5th centuries CE), the Middles Ages (7th-16th centuries CE) and the Modern Period (16th-18th centuries CE). Sex-ratios are provided as the proportion of males (blue) identified in each category. The proportion of females is shown in orange. The total numbers of remains included in the analysis are also reported. *: Statistical significance.

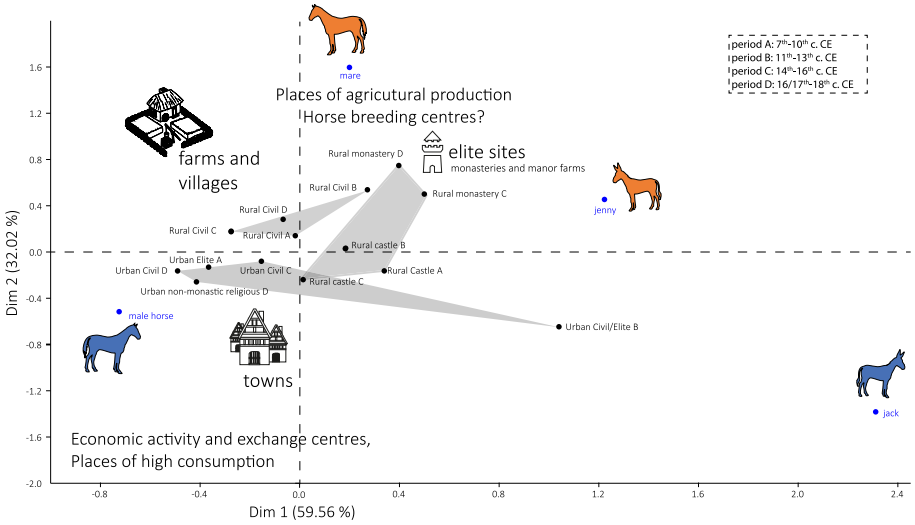

Fig. 4. Factorial analysis of horse and donkey sex-ratios within various social contexts.

young foals and fillies, rather than isolated bachelors, which was further confirmed for other sites located in Southwestern France (Feyfant et al., 2015). While the amount of sequence data generated in this study precludes any investigation of familial relationships, they support balanced sex-ratios both in natural (Igue du Gral) and anthropic contexts. This is in line with previous reports applying a similar methodology to Late Pleistocene equine material from Belgium and Siberia (Fages et al., 2020) and confirms hunting strategies not targeting bachelor groups. Interestingly, with four mares and one male identified at the Magdalenian camp of Etiolles, our data also confirm previous contention that the horse assemblage was formed following a single hunting episode of a single-family group showing a harem-like structure (Bignon, 2006).

4.2. *Iron Age and Roman sacrificial rituals*

Overall, our analyses are in accordance with earlier reports

supporting male-biased representation in pan-Eurasian archaeological remains from the early Bronze Age (Fages et al., 2020). The new data analyzed in this study, however, reveals more subtle sex distribution patterns at the more local scale and according to the archaeological context (i.e. habitat *vs* ritual).

A fraction of the Iron Age material examined here comes from well-established sacrificial sites, such as Vertault, Le Cendre-Gondole, Orcet and Saint-Just-en Chaussée 94–95. It also includes sites where the presence of sacrificial ritual practice is considered likely (Thézy-Glimont), or suggestive (Pech Maho). Combined, and despite archaeological evidence supporting diverse practices across sites and time periods, they illustrate the central religious role that horses played at the time in Gauls.

Interestingly, our data indicate that horse sacrifice was preferentially, and sometimes even exclusively, oriented towards males. This is reminiscent of practices reported in other Iron Age contexts, such as Pazyryk Scythian burials from the Altay region (Lepetz, 2013; Librado et al., 2017; Lepetz et al., 2020), but also of more recent contexts, such as Viking tombs in Northwestern Europe (Nistelberger et al., 2019). The over-representation of horse males may simply reflect ritual decisions purely oriented according to the sex of the animals. Interestingly, similar decisions could also prevail for some of the other species sacrificed at the same sites, such as the dozens of dog males found at Vertault (Méniel and Jouin, 2000). Alternatively, the over-representation of males may reflect the indirect consequences of a generally particular status that males had at the time, e.g. in relation to mounting, prestige and wars. Regardless, our work reveals that such sacrificial practices were not limited to the Iron Age in France but also extended to the Roman Period. Indeed, the site from Longueil-Sainte-Marie (L'Orméon) is considered to represent a local, rural sanctuary that was linked to a sacred natural humid zone, with evidence including miniature ceramics associated with an important accumulation of equine bones, derived from at least 40 individuals (Gaudefroy and Lepetz, 2000). Remains from a total of 26 of these individuals showed DNA preservations compatible with taxonomic and sex identification. Our data revealed that only horse males were deposited, even though other contemporary archaeological sites not associated with ritual activities showed substantial proportions of mules (Lepetz et al., 2021). This finding reinforces previous interpretations of the Longueil-Sainte-Marie site as ritual.

4.3. Males in the city

By revealing that males were strongly over-represented in cities, our work provides the first archeozoological evidence supporting sex-biased factors shaping the organization of equine husbandry in France during Antiquity, the Middle Ages and the Modern Period. Equine sex-ratios indeed reached approximately ~ 88.6% in Antique urban contexts *versus* only ~ 54.5% in rural contexts. Horse males also appeared central to the economy of Medieval and Modern cities, where they represented approximately ~ 70.6% of the bone assemblages. In contrast, females were proportionally more abundant in rural contexts, and for donkeys, even balanced in numbers with males.

Following the work from historians (Bautier and Bautier, 1980), increased proportions of mares provide a robust marker for breeding. Importantly, many of the rural sites analyzed represent villages that were under the control of abbeys (e.g. '*Rue du bois Tillet*' at Crépy-en-Valois, where the abbey was built during the 10th century CE (Gnat, 2002)). The large abbeys and civil elite context sites investigated here were also mostly located into the fertile regions of Picardy and Pays-de-France, where the horse was paramount to local economies, both used in agriculture along with the plough since at least 1100 CE (Fossier, 1968) and in relation to military activities (Prévot and Ribémont, 1994). Although this remains speculative, the increased concentrations of females observed at locations associated with power may reflect intentional control by the social elites over horse reproductive resources at a time when the animal was not only expensive but also a military asset, providing, thus, both a social marker and a commodity for exercising power, reinforcing social dominance. Sites such as Boves and Démuin (Picardy), Saint-Sornin (Charente-Maritime) and Châtenois and Saverne (Alsace) would then offer typical examples of such production centers where control and breeding were organized.

In Gallo-Roman cities, the sites investigated include many relegation zones in which animal carcasses were evacuated, accumulated and reused for their bones, skins and tendons (e.g. Chartres, Evreux '*Clos-aux-Duc*'; Lepetz et al., 2013). These accumulations are particularly illustrative of the animals participating to the city life and only consist of adult, often old, animals (Lepetz et al., 2013). Carcass recycling for bones, skins and tendons was particularly well organized and effective from the Middle Age, and comprised all kinds of animals, including reform animals displaying abundant skeletal pathologies characteristic of particularly hard work conditions (Barme and Clavel, 2015; Deborde and Bandelli, 2017). It is likely that living in such difficult conditions would have compromised the female fitness. Therefore, females may have also been preferentially maintained in rural contexts to decrease the risk of miscarriage and, thus, sustain production demands. Medieval hippiatric treaties time and again urge horse breeders to separate gravid mares from stallions, monitor feeding and pay attention to cold temperatures (Rusio, 1583). This is also true for later textual documents, such as the '*Théâtre d'agriculture*', first published in 1600 CE and re-edited until the 19th century CE (de Serres 1804–1805), but may have equally applied to Antiquity as Varro already recommended that gravid females are spared from work (Varro 7.2). The fact that weaning and training did not generally start before two and three years after birth, respectively (Rusio, 1583), may also have motivated the keeping of females away from cities. Additionally, the presence of females in cities during the breeding season may not be fit to the urban environment, as female heats can cause bouts of tension (Marcenac and Aublet, 1964) and may have caused diminishing returns for working males.

Combined, all these factors may underpin the strong bias towards males reported here for both Roman and Medieval cities, and the marked difference in the management of equine resources observed between rural and urban contexts. These depict an urban economy fueled by adult, often old, males, and rural environments where females and subadults of both sexes were maintained to sustain production demands.

Finally, it should be stressed that urban environments were also extremely stressful for males. In addition to the considerable numbers of skeletal pathologies found in the archaeological record (Barme and Clavel, 2015), textual sources insist on the importance of getting animals used to ambient noise (e.g. see Pierre de Crescent's '*Opus ruralium commodorum*' published in 1492, and cited by Prévot and Ribémont, 1994). Such environments may have proved particularly challenging for those most nervous animals and breeds. Although this remains to be demonstrated genetically, more tempered animals from cold blood breeds may have, thus, been preferred. It is also likely that a large fraction of the males identified were castrated, as gelding is a practice known for increasing docility that is already reported in Roman sources (Varron, 2, 7, 15; Peters, 1998; Gitton-Ripoll, 2016), and common to many Medieval hippiatric treaties (Poulle-Drieux, 1966; Ligneureux, 2005; Prévot and Ribémont, 1994). Methods aimed at the detection of geldings, possibly scrutinizing bone remodeling patterns as a result of increased muscular mass (Luff, 1994; Davis, 2000), or perhaps leveraging differentially methylated markers (Hanghøj and Orlando, 2018) in stallions and geldings, should be developed to confirm this hypothesis and determine when and in which contexts, this practice was first applied to horses.

Author contributions

BC, SL and LO designed research. BC, SL, JMA, MB, PB, MO, OBL, JCC, MBM, NB, AB, FD, SFo, SFr, AG, GJ, CM, NM, ANE, AP, OP, JR, OR, MS, SVL, CV, JHV, PW and LO provided material and reagents. LC, SS,

LTC, XL, AF, NK, ASO, CDS, PC, OA and CG performed ancient DNA experiments. LC, SS, LTC, ASO, JMA, AP and PW carried out and/or coordinated DNA sequencing. DA and LO performed sequences analyses. BC, SL and LO interpreted the results, with input from all co-authors. LO coordinated the study. SL, BC and LO wrote the manuscript, with input from all co-authors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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