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Equids (*Equus sp.*) in southern Spain from the Palaeolithic to the Bronze Age

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ABSTRACT: The genus *Equus* was represented on the Iberian Peninsula by four species during the late Quaternary: the wild, now extinct, *E. ferus* (wild horse) and *E. hydruntinus* (European wild ass) and the extant, domestic *E. caballus* (horse) and *E. asinus* (donkey). The distribution and timing of the extinctions of the wild species and arrival of the domestic species is important to understand the changing environment and cultures through this dynamic period in one of the three southern Pleistocene glacial refugia in Europe. Here we collected data from all zooarchaeological studies that meet basic completeness criteria from the Palaeolithic to the Bronze Age (45–3.2 ka BP) and analysed the equine data in light of other large mammals at the same sites in order to document the species turnover and distributions through this culturally and ecologically dynamic period. The vast majority of Palaeolithic *Equus* were confidently identified as *E. ferus*, and by the Bronze age as *E. caballus*, with much uncertainty in between. Over time the larger equids (horses) were much more common than the smaller equids (asses). Equids were not common, but they were distributed across the southern Iberian peninsula through the Chalcolithic, and then appear to have become restricted to the drier eastern region in the Bronze Age. These analyses indicate that both *E. ferus* and *E. hydruntinus* went extinct by the end of the Pleistocene/Palaeolithic in Andalucia. Not all communities maintained equal numbers of equids, and their distribution changed with the changing climate through time, most notably between the Chalcolithic and the Bronze Age when confidence in species identification and local density of horses increase, but the distribution is restricted to the drier eastern region. © 2023 The Authors *Journal of Quaternary Science* Published by John Wiley & Sons Ltd.

KEYWORDS: Andalucia; European wild ass; horse; Iberia; mule

Introduction

Two wild equids (*Equus* sp.) inhabited the Iberian peninsula in the late Pleistocene, the larger *Equus ferus*, the wild horse, and the smaller and much more rare *E. hydruntinus* or European wild ass (Sanz-Royo et al., 2020). Both of these species went extinct on the Iberian peninsula by the late Pleistocene or early to mid-Holocene (Geigl and Grange, 2012; Crees and Turvey, 2014). The wild horse declined notably across Europe at this time (Bendrey, 2012), although some think it survived to historic times in the forests of Germany, Lithuania, Poland, Ukraine and Russia (Olsen, 2006), although that seems unlikely (Lovász et al., 2021). By the Chalcolithic (5.5–4 ka BP) there were again two equids on the Iberian peninsula, but they were both domestic: the larger and more common domestic horse, *E. caballus*; and the smaller donkey, *E. asinus* (Cardoso et al., 2013).

The wild horse *E. ferus* was widespread across Eurasia and North America, and is the ancestral species of the domestic horse (Vilà et al., 2001; Gaunitz et al., 2018). There was some genetic structure in Pleistocene wild horses across their distribution based on ancient mitochondrial DNA sequences (Vilà et al., 2001; Cieslak et al., 2010), but there was apparent panmixia across much of Eurasia. The earliest evidence of horse domestication comes from about 5.5 ka BP in the central Asian Neolithic (Olsen, 2000; Outram et al., 2009; Gaunitz et al., 2018). However, genetic studies suggest that wild horses from multiple locations contributed to the domestication process, either through independent domestications or backcrossing (Fages et al., 2019; Jansen et al., 2002; Leonard and Vilà, 2014; Lira et al., 2010; Lira, 2017; Vilà et al., 2001). Genetic studies also suggest that ancient Iberian horses could have been one of the multiple populations that contributed to the domestic species (Vega-Pla et al., 2006; Warmuth et al., 2011; Fages et al., 2019). The wild ancestor of the donkey (*E. africanus*) is not native to Europe; it is only distributed in Africa (Beja-Pereira et al., 2004; Rossel et al., 2008; Vilà et al., 2006).

The change from wild *E. ferus* and *E. hydruntinus* to the domestic *E. caballus* and *E. asinus* is difficult to identify in the archaeological record owing to high within-species morphological variability in equids in general (Bignon and Eisenmann, 2006; Eisenmann, 1996). Many zooarchaeological studies are only able determine equids to the genus level, and sometimes genus and size class (large or small referring to horse or donkey, respectively, without determining the species). A further complication in the archaeological record is the ability of horses and donkeys to hybridize and yield morphologically intermediate mules (Lau et al., 2009; Granado et al., 2020).

The Iberian peninsula was one of the natural Pleistocene refuges for European fauna and flora (Crees and Turvey, 2014; Morales et al., 1996), and there is genetic evidence that Iberian horses were isolated from the broader Eurasian horse population

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in the late Pleistocene and early Holocene (Cieslak et al., 2010). Despite the added importance of this population, there is a dirth of published palaeobiological studies of the horses on the Iberian Peninsula, especially from the south, Andalucia (Sommer et al., 2011; Crees and Turvey, 2014; Strani and DeMiguel 2023). This problem is aggravated by the difficulty of finding papers that were printed in regional, not scientifically indexed publications (Bernáldez-Sánchez and Bernáldez-Sánchez, 1998; García-Viñas and Bernáldez-Sánchez, 2013; García-Viñas et al., 2014). During the 1970s and 1980s there was considerable archaeological effort made in Andalucia, but most of the reports were published in books that have not yet been digitized, or other local, undigitized literature. To facilitate access to these data, the Andalusian Historical Heritage Information System (Sistema de Información para la Gestión del Patrimonio Cultural en Andalucía; Mosaico) registers the information of all approved archaeological sites in the province.

Here we characterize changes in the distribution and relative abundance of the equid species in Andalucia from the Middle–Upper Palaeolithic (late Mousterian) to the Bronze Age (45–3.2 ka BP). This period starts when all equids were clearly wild, and ends after all equids in the region are clearly domestic. We used the Mosaico database to identify all archaeological sites in Andalucia in the target time period, georeferenced all sites, determined which sites had associated zooarchaeological data, extracted ungulate faunal data, and measured equid first phalanges where possible, and then analysed the spatio-temporal distribution of these four species of *Equus*.

Materials and methods

Archaeological sites

The sites included in this study were identified through the Mosaico database. Mosaico was developed as a centralized registry of all approved archaeological excavations in the province because many of the reports and publications were difficult to locate as they were published in a wide variety of venues including local non-indexed, non-digitized books and reports. Mosaico registers the information of more than 14 000 archaeological sites in this region (June 2017) including locality, responsible researcher and publications including reports. Mosaico is publicly available on the internet (https://juntadeandalucia.es/organismos/turismoculturaydeporte/areas/cultura/bienes-culturales/recursos-difusion-patrimonio/paginas/mosaico.html). This database is available only in Spanish. There are 4342 archaeological sites recorded in Mosaico dating from the Middle–Upper Palaeolithic to the Bronze Age (Fig. 1). Only a small percentage of these include zooarchaeological analyses. We analyse faunal data from all Andalusian archaeological sites in Mosaico for the period from the late Mousterian to late Bronze age which include zooarchaeological surveys (Table 1). We compiled location and reference data for each archaeological site and information about the province, town, name of the site and its geographical coordinates in addition to the faunal information. Most of the archaeological sites are dated according to the culture identified; only a few have been ^{14}C dated. All these data were located using ArcGIS 9.3.1. A single site may be divided into multiple registers, which correspond to different time periods. The registers are grouped into the four prehistoric periods studied on the Iberian Peninsula: the Middle–Upper Palaeolithic (45–13.7 ka BP), the Neolithic (8–5.5 ka BP), the Chalcolithic (5.5–4 ka BP) and the Bronze Age (4–3.2 ka BP). The unit of analysis is the register.

Taxonomy and morphology

Taxonomic identification was generally taken from the report or publication for all wild and domestic ungulates, and recognized taxonomic names are used here (Wilson and Reeder, 2005). It

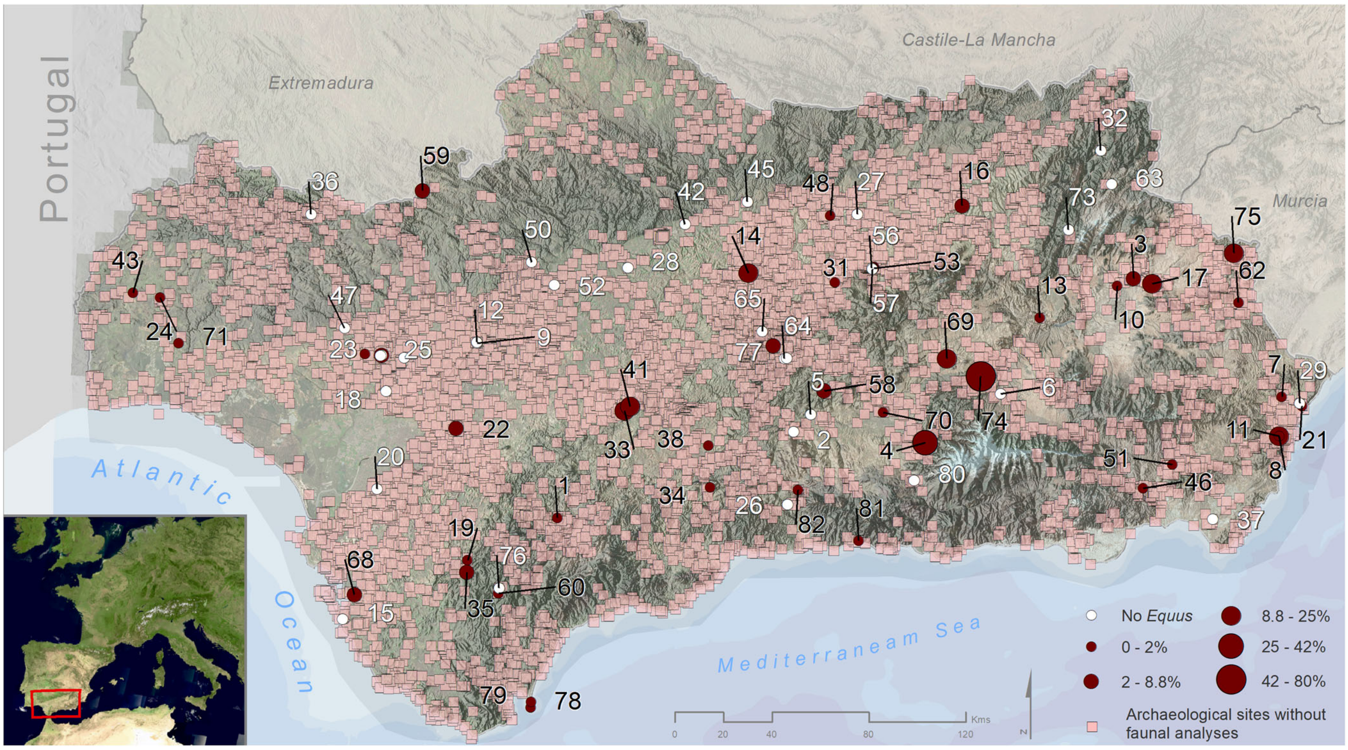

Figure 1. Map of Andalucia showing the location of all Middle–Upper Palaeolithic to Bronze Age archaeological sites identified. Sites marked with a square do not have zooarchaeological data, while those marked with circles do. Sites marked with a white circle do not contain equids, while those marked with a red circle do. Sites with zooarchaeological data are labelled with numbers that correspond to those in Table 1. [Color figure can be viewed at wileyonlinelibrary.com]

Table 1. Andalusian archaeological sites dated to between the Palaeolithic and the Bronze Age with published archaeozoological studies. Site no. refer to labels in the maps in Figs 1–5.

Site no.	Archaeological Site	Locality	Province	Culture	Reference(s)
1	Acinipo	Ronda	Málaga	Bronze Age	Riquelme, 1994; Riquelme & Aguayo, 2000
2	Alcazaba	Loja	Granada	Bronze Age	Pachón et al., 2013
3	Castellón Alto	Galera	Granada	Bronze Age	Milz, 1986
4	Cerro de la Encina	Monachil	Granada	Bronze Age	Friesch, 1987
5	Cerro de los Castellones	Laborcillas	Granada	Bronze Age	Driesch & Kokabi, 1977
6	Cuesta del Negro	Purullena	Granada	Bronze Age	Lauk, 1976
7	Fuente Álamo	Cuevas del Almanzora	Almería	Bronze Age	Manhart et al., 2000
8	Gatas	Turre	Almería	Bronze Age, Chalcolithic	Montón, 1999
9	General Freire 12	Carmona	Sevilla	Bronze Age	Belén et al., 2000
10	Loma de la Balunca	Castilléjar	Granada	Bronze Age	Milz, 1986
11	Peñalosa	Turre	Almería	Bronze Age	Sanz & Morales, 2000
12	Plaza de Santiago 6-7	Carmona	Sevilla	Bronze Age	Belén et al., 2000
13	Terrera del Reloj	Dehesas de Guadix	Granada	Bronze Age	Milz, 1986
14	Torreparedones	Baena	Córdoba	Bronze Age	Hamilton, 1999
15	El Estanquillo	San Fernando	Cádiz	Bronze Age	Bernáldez-Sánchez, 2009
16	Las Eras	Úbeda	Jaén	Bronze Age, Chalcolithic	Riquelme, 2009
17	Cerro de la Virgen	Orce	Granada	Bronze Age, Chalcolithic	Driesch, 1972
18	Cerro de San Juan	Coria del Río	Sevilla	Bronze Age, Chalcolithic	García-Viñas et al., 2018
19	Cueva de la Dehesilla	Algar	Cádiz	Bronze Age, Chalcolithic, Neolithic	Boessneck & Driesch, 1980a; Morales & Riquelme, 2004; García-Rivero et al., 2019
20	Calle Alcazaba	Lebrija	Sevilla	Bronze Age, Chalcolithic, Neolithic	Bernáldez-Sánchez & Bernáldez-Sánchez, 2000
21	Almizaraque	Cuevas del Almanzora	Almería	Chalcolithic	Delibes de Castro et al., 1996
22	Amarguillo II	Los Molares	Sevilla	Chalcolithic	Cabrero et al., 2006
23	Barrio metalúrgico	Valencina de la Concepción	Sevilla	Chalcolithic	Abril et al., 2010
24	Cabezo Juré	Alosno	Huelva	Chalcolithic	Nocete et al., 1999; Riquelme, 2004
25	Calle Mariana Pineda	Valencina de la Concepción	Sevilla	Chalcolithic	Pajuelo & López, 2013
26	Cerro de Capellanía	Vélez-Málaga	Málaga	Chalcolithic	Bernáldez-Sánchez, 2009
27	Cerro de la Coronilla I and II	Cazalilla	Jaén	Chalcolithic	Nocete, 1994
28	Cerro de la Horca II and III	Guadalcázar	Córdoba	Chalcolithic	Nocete, 1994
29	Cerro de la Virtud	Cuevas del Almanzora	Almería	Chalcolithic	Domínguez-Rodrigo, 2001
30	Cerro de la Cabeza	Valencina de la Concepción	Sevilla	Chalcolithic	Hain, 1982
31	Ciudad de la Justicia	Jaén	Jaén	Chalcolithic	Riquelme, 2010
32	Cortijo de la Torre	Hornos de Segura	Jaén	Chalcolithic	Nocete, 1994
33	Cueva Antoniana	Gilena	Sevilla	Chalcolithic	Bernáldez-Sánchez, 2009
34	Cueva del Toro	Antequera	Málaga	Chalcolithic	Watson et al., 2004
35	Cueva Higueral de Valleja	Arcos de la Frontera	Cádiz	Chalcolithic, Neolithic	Cáceres, 1997
36	Dolmen Valdelinares	Zufre	Huelva	Chalcolithic	Romero, 2001a
37	El Barranquete	El Barranquete	Almería	Chalcolithic	Almagro, 1973; Driesch, 1973
38	El Sililllo	Antequera	Málaga	Chalcolithic	Fernández et al., 2014
39	Parcela Municipal	Valencina de la Concepción	Sevilla	Chalcolithic	Bernáldez-Sánchez et al., 2012
40	Gilena 86	Gilena	Sevilla	Chalcolithic	Bernáldez-Sánchez, 2009
41	Gilena 89	Gilena	Sevilla	Chalcolithic	Bernáldez-Sánchez, 2009
42	Iglesia antigua	Alcolea	Córdoba	Chalcolithic	Martínez, 2013
43	Junta de los Ríos	Puebla de Guzmán	Huelva	Chalcolithic	Abril et al., 2007; Nocete et al., 2009
44	La Gallega	Valencina de la Concepción	Sevilla	Chalcolithic	Bernáldez-Sánchez et al., 2013
45	Llanete de los moros	Montoro	Córdoba	Chalcolithic	Liesau, 2000
46	Los Millares	Santa Fé de Mondújar	Almería	Chalcolithic	Navas et al., 2005
47	Los Páramos	Aznalcóllar	Sevilla	Chalcolithic	Bernáldez-Sánchez & García-Viñas, 2010
48	Los Pozos	Lahiguera	Jaén	Chalcolithic	Nocete, 1994
49	Parque Miraflores	Sevilla	Sevilla	Chalcolithic	Lara et al., 2004
50	Puerto Palmera	La Puebla de los Infantes	Sevilla	Chalcolithic	Romero, 2001b
51	Terrera Ventura	Almería	Almería	Chalcolithic	Driesch & Morales, 1977
52	Veruga alta	Palma del Río	Córdoba	Chalcolithic	Martínez, 2013

(*Continued*)

Table 1. (*Continued*)

Site no.	Archaeological Site	Locality	Province	Culture	Reference(s)
53	G. Triviño	Jaén	Jaén	Chalcolithic	Riquelme et al., 2012
54	Tramo 3	Jaén	Jaén	Chalcolithic	Riquelme et al., 2012
55	Subestación	Jaén	Jaén	Chalcolithic	Riquelme et al., 2012
56	P. Estación	Jaén	Jaén	Chalcolithic	Riquelme et al., 2012
57	Ronda Paz	Jaén	Jaén	Chalcolithic	Riquelme et al., 2012
58	Los Castillejos	Montefrío	Granada	Chalcolithic, Neolithic	Ziegler, 1990; Riquelme, 1998; Morales & Riquelme, 2004
59	Santiago Chica 76-80	Cazalla de la Sierra	Sevilla	Chalcolithic, Neolithic	Morales & Riquelme, 2004; Bernáldez-Sánchez, 2009
60	Cueva Parralejo	San José del Valle	Cádiz	Chalcolithic, Neolithic	Morales & Riquelme, 2004
61	Corte Inglés	Jaén	Jaén	Chalcolithic-Neolithic	Riquelme et al., 2012
62	Cerro de Los López	Vélez-Rubio	Almería	Neolithic	Riquelme, 2003
63	Cueva de El Nacimiento	Pontones	Jaén	Neolithic	Alférez et al., 1981; Asquerino, 1984; Boessneck & Driesch, 1980b
64	Cueva de los mármoles	Priego de Córdoba	Córdoba	Neolithic	Asquerino, 1987
65	Cueva de los Murciélagos	Zuheros	Córdoba	Neolithic	Vicent & Muñoz, 1973
66	Plaza del Palenque	Priego de Córdoba	Córdoba	Neolithic	Morgado et al., 2015
67	Castillo de Doña Mencía	Doña Mencía	Córdoba	Neolithic	Martínez & Vera-Rodríguez, 2017
68	El Retamar	Puerto Real	Cádiz	Neolithic	Cáceres, 2002
69	La Carigüela	Píñar	Granada	Palaeolithic, Neolithic	Bouchud, 1969*; Villar, 1998; Morales & Riquelme, 2004; Samper, 2010
70	La Molaina	Pinos Puente	Granada	Neolithic	Morales & Riquelme, 2004
71	Papa Uvas	Aljaraque	Huelva	Neolithic	Morales, 1985; Álvarez & Chaves, 1986
72	Polideportivo de Martos	Martos	Jaén	Neolithic	Riquelme et al., 2012
73	Valdecuevas	Cazorla	Jaén	Neolithic	Sarrión, 1980
74	Cueva Horá	Darro	Granada	Palaeolithic	Martín-Penela, 1986
75	Cueva de Ambrosio	Vélez-Blanco	Almería	Palaeolithic	Ripoll, 1986; Yravedra, 2007
76	Cueva Higueral de Motillas	Jerez de la Frontera	Cádiz	Palaeolithic	Cáceres & Anconetani, 2002
77	Cueva de El Pirulejo	Priego de Córdoba	Córdoba	Palaeolithic	Asquerino & Riquelme, 2006; Riquelme, 2008
78	Cueva de Gorham	Gibraltar	Gibraltar	Palaeolithic	Zeuner & Sutcliffe, 1964; Rodríguez-Vidal et al., 2010; Riquelme et al., 2011
79	Devil's Tower	Gibraltar	Gibraltar	Palaeolithic	Bate, 1928
80	Cueva de los Ojos	Cozvijar	Granada	Palaeolithic	Almohalla & Toro, 1985
81	Cueva de Nerja	Nerja	Málaga	Bronze Age, Chalcolithic, Neolithic, Palaeolithic	Morales & Martín, 1995; Riquelme et al., 2005-2006
82	Cueva de Zafarraya	Alcaucín	Málaga	Palaeolithic	Barroso et al., 2003, 2006; Monclova et al., 2012
83	Sima de Abraham	Priego de Córdoba	Córdoba	Palaeolithic	Martínez et al., 2010

can be difficult to differentiate equid species based only on fragmentary skeletal remains (Morales et al., 1996). Where the author mentions the presence of unspecified 'horses', we list them as *Equus* sp. There have been some taxonomic revisions, perhaps most interestingly the correction by Uerpmann (2005) of two *E. asinus* bones published as *E. hydruntinus* (Driesch, 2000) for the archaeological site of Cerro de la Virgen (Granada). Where possible, we took from the literature or measured the length and width of the equid first phalanges from these sites (Supporting Information Table S1). Measurements were also taken from modern (n = 10) and more recent archaeological sites (n = 14) for reference.

Statistics

Following Bernáldez-Sánchez et al. (2017), remains of adult equids are in Class I, species whose adult body mass is more than 200 kg, or Class II, species whose adult body mass is between 18 and 200 kg. This simplifies statistical assumptions because Class I and Class II vertebrate taxa should be represented in the taphocoenosis unless: (i) they are not present in the community, (ii) the size of their populations is very low or (iii) the deposit only contains some species selected by humans (Bernáldez-Sánchez 2009; 2011). The minimum number of specimens (NISP) of Class I and Class II ungulates was calculated for each register (time period/site). The frequency of horses was calculated by dividing the NISP of equids by the NISP of all Class I and Class II ungulates, per register.

Results

Sites

Of the archaeological sites identified based on the criteria of area (Andalucia) and time period (Middle–Upper Palaeolithic to the Bronze Age) in the Mosaico database (n = 4342; Figs 1–5), many had been analysed for multiple time periods yielding almost twice as many registers as sites (n = 7553; Table 2). Of these, less than 2% of the sites (n = 82) or registers (n = 97) had documented the associated fauna (Table 2). Of those that did report the fauna, about half of the sites (n = 49) and registers (n = 54) recorded at least one species of *Equus*. The total number of skeletal remains from

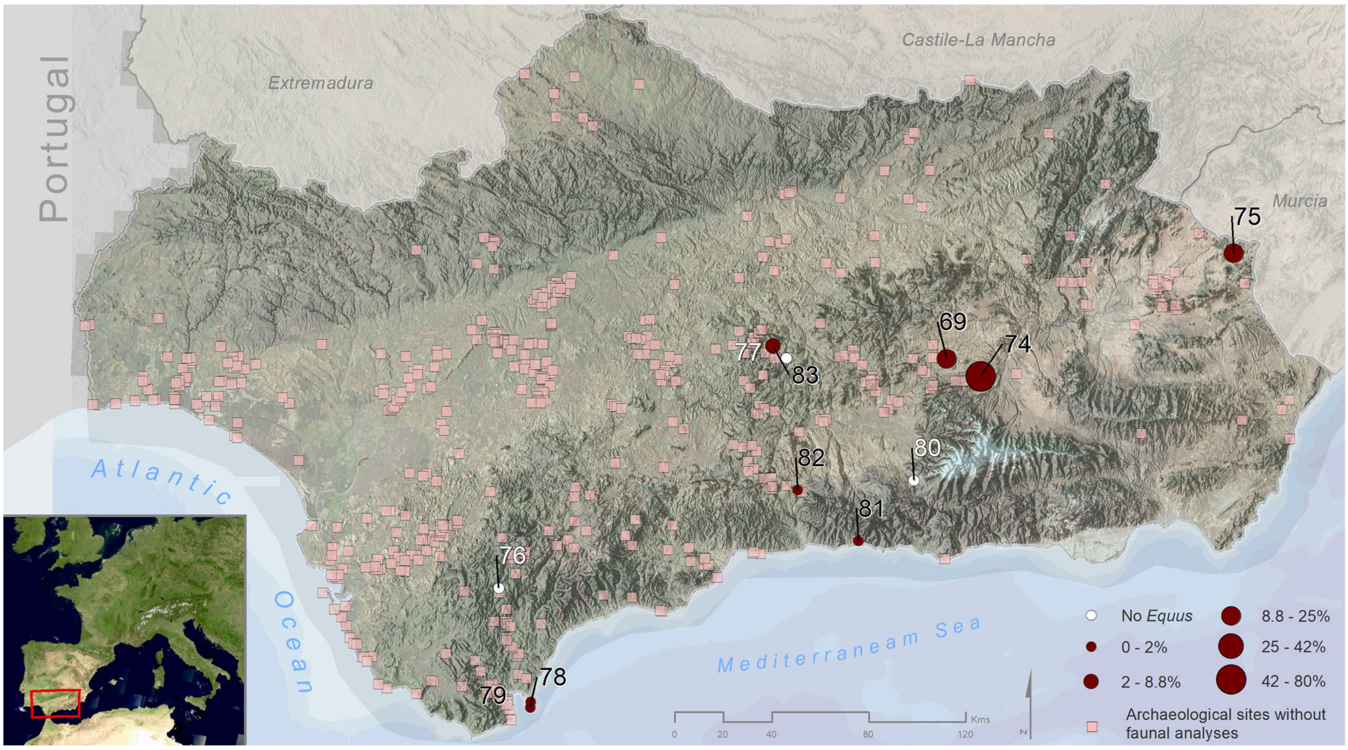

Figure 2. Map of Andalucia showing the location of all Palaeolithic archaeological sites identified. Sites marked with a square do not have zooarchaeological data, while those marked with circles do. Sites marked with a white circle do not contain equids, while those marked with a red circle do. Sites with zooarchaeological data are labelled with numbers that correspond to those in Table 1. [Color figure can be viewed at wileyonlinelibrary.com]

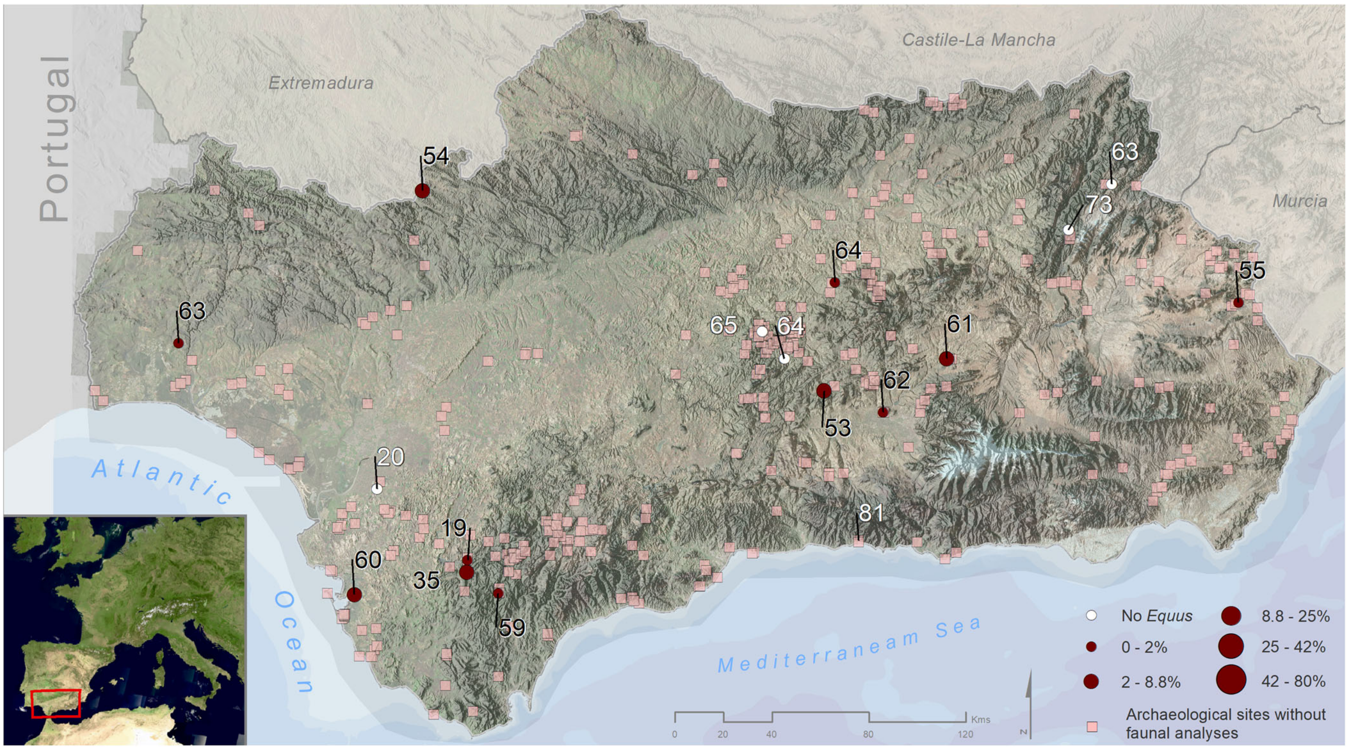

Figure 3. Map of Andalucia showing the location of all Neolithic archaeological sites identified. Sites marked with a square do not have zooarchaeological data, while those marked with circles do. Sites marked with a white circle do not contain equids, while those marked with a red circle do. Sites with zooarchaeological data are labelled with numbers that correspond to those in Table 1. [Color figure can be viewed at wileyonlinelibrary.com]

non-human Class I and Class II animals in the 54 records is 183 273 bones. The sites are not evenly distributed through time (Table 2), with the most recent time period, the Bronze Age, being most heavily represented. There is a gap in the record, an absence of sites, from around 13.7 to 8 ka BP.

Equid presence and distribution

A high percentage of the Palaeolithic registers with fauna studied have equid bones (90%; Table 3), which declines in the Holocene (Table 3). The period with the lowest frequency of equid presence is the Chalcolithic (48%; Table 3). The

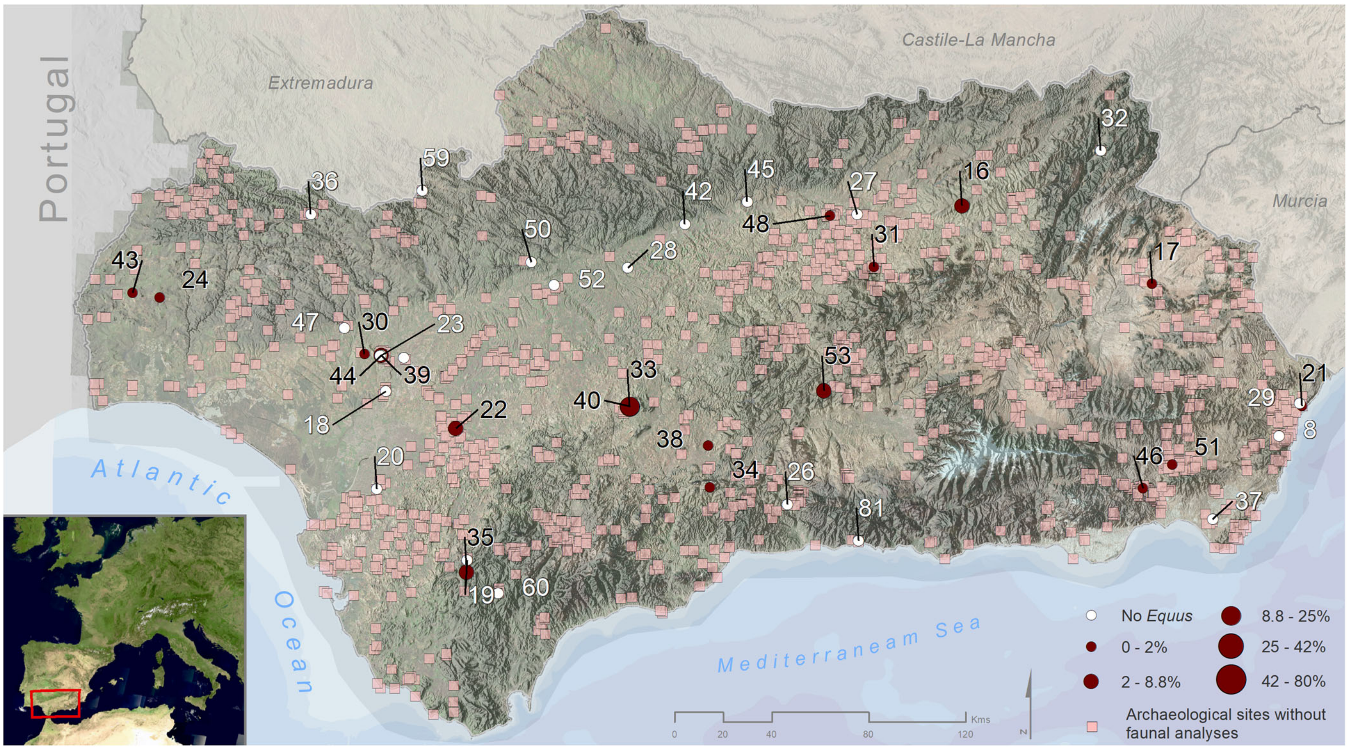

Figure 4. Map of Andalucia showing the location of all Chalcolithic archaeological sites identified. Sites marked with a square do not have zooarchaeological data, while those marked with circles do. Sites marked with a white circle do not contain equids, while those marked with a red circle do. Sites with zooarchaeological data are labelled with numbers that correspond to those in Table 1. [Color figure can be viewed at wileyonlinelibrary.com]

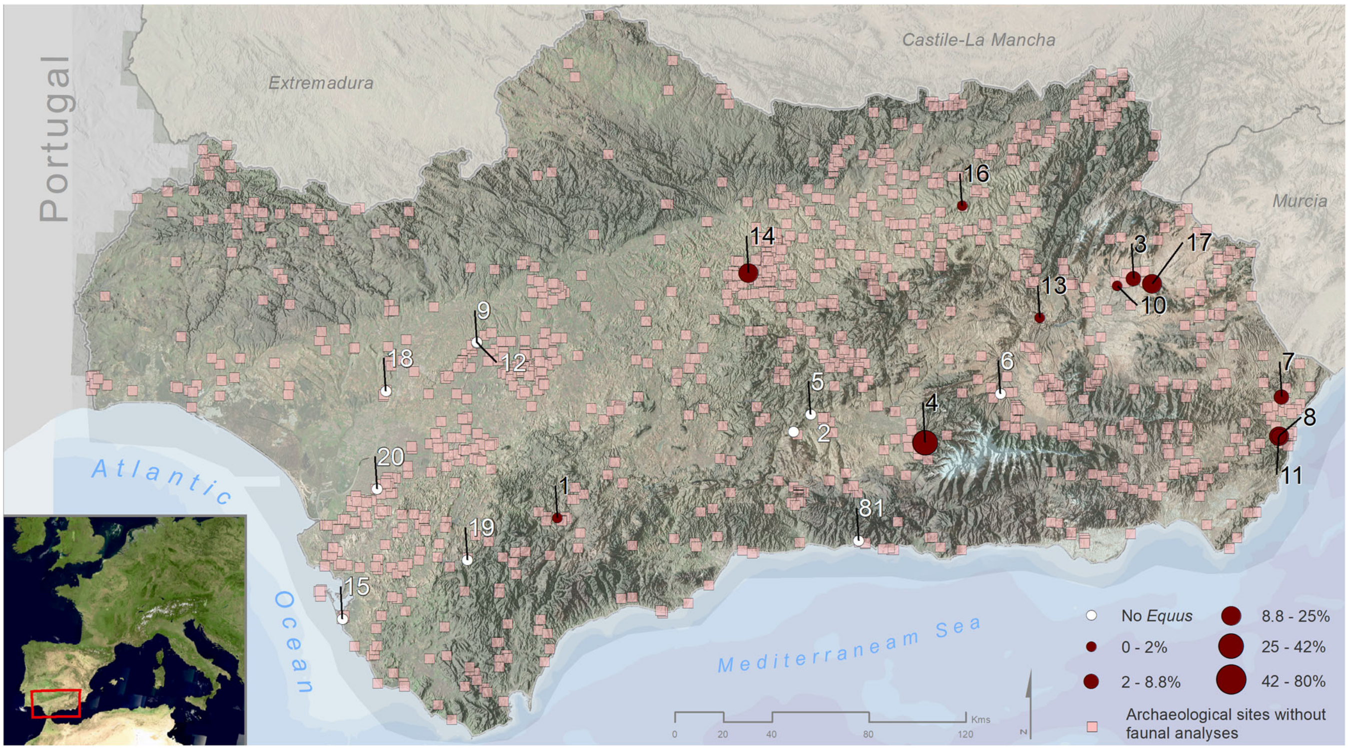

Figure 5. Map of Andalucia showing the location of all Bronze Age archaeological sites identified. Sites marked with a square do not have zooarchaeological data, while those marked with circles do. Sites marked with a white circle do not contain equids, while those marked with a red circle do. Sites with zooarchaeological data are labelled with numbers that correspond to those in Table 1. [Color figure can be viewed at wileyonlinelibrary.com]

frequency of equid remains in a site also changes through time, with 8.2% of the Class I and Class II ungulate bones corresponding to equines in the Palaeolithic, but only 1% (Neolithic and Chalcolithic) to 3% (Bronze Age) in later periods (Table 3). In summary, in recent prehistory, there are relatively fewer deposits with any horse bones at all, and in deposits where they are present, they are less frequent than in the oldest Palaeolithic deposits.

Table 2. Overview of archaeological registers (time period/site) in Andalucia registered in Mosaico (Sistema de Información para la Gestión del Patrimonio Cultural en Andalucía) per time period with how many records have had the zooarchaeological material identified, and of those how many contain any identified equid remain(s). The minimum number of individuals (NISP) of all Class I and II ungulates other than *Equus* and just equids is shown.

	Palaeolithic	Neolithic	Chalcolithic	Bronze Age	Total
Archaeological registers	603	1037	2643	3270	7553
Faunal registers	10	18	48	21	97
Equus registers	9	11	23	11	54
NISP Classes I and II	9527	10 289	85 561	77 896	183 273
NISP *Equus*	784	133	689	2359	3965

Table 3. Overview of archaeological registers (time period/site) registered in Mosaico. The total number of registers per time period considered here, how many of those have the zoological material characterized (Faunal registers), the percentage of registers that have had the fauna analysed (% Faunal registers), how many of the faunal registers record any equid (*Equus* registers) and the percentage of records with fauna studied that have equids (% *Equus* registers). The total minimum number (NISP) of Class I and II ungulates identified in all registers per time period (NISP Classes I and II), the minimum number of equids per time period (NISP *Equus*), and the percentage of Class I and Class II ungulate remains that are equids (% NISP *Equus*).

	Palaeolithic	Neolithic	Chalcolithic	Bronze Age	Total
Archaeological registers	603	1037	2643	3270	7553
Faunal registers	10	18	48	21	97
% Faunal registers	1.7	1.7	1.8	0.6	1.3
Equus registers	9	11	23	11	54
% *Equus* registers	90	61	48	52	56
NISP Classes I and II	9527	10 289	85 561	77 896	183 273
NISP *Equus*	784	133	689	2359	3965
% NISP *Equus*	8.2	1.3	0.8	3.0	2.2

Table 4. Equid remains from the different time periods in Andalucia. The number and percentage of equid remains per species per time period, and the percentage of the Class I and Class II identified ungulate remains in Andalucia identified as *Equus* per time period and in total.

	Palaeolithic	Neolithic	Chalcolithic	Bronze Age	Total
E. ferus	720 (92%)	0	36 (5%)	0	756
Equus sp.	15 (2%)	110 (83%)	567 (83%)	12 (0.5%)	704
E. caballus	0	20 (15%)	82 (10%)	2347 (99%)	2449
E. hydruntinus	49 (6%)	0	1 (0.3%)	0	50
E. asinus	0	3 (2%)	3 (0.6%)	0	6
Total *Equus*	784	133	689	2359	3965
Total Classes I, II	9527	10 289	85 561	77 896	183 273
% *Equus*	8.2	1.3	0.8	3.0	2.2

Equid species through time

Overall in our sample of 183 273 identified Class I and II non-human bones, 3965 were identified as equids. Of those, 2449 domestic horse bones were identified, 756 wild horse remains, 50 wild ass, six domestic donkey and 704 equid remains without a specific determination (Table 4). The Palaeolithic sites are composed of wild species (*E. ferus* and *E. hydruntinus*), and the Neolithic to Bronze Age record contains domestic species. The wild horse, *E. ferus*, is represented by 19% of the equine bones (Table 4), the majority of which (92%) were found at Cueva Horá (Granada, SE Andalucia; Martín-Penela, 1986) and Cueva de Ambrosio (Almería, SE Andalucia; Ripoll, 1986; Jordá et al., 2012; Yravedra, 2007), sites from the Mousterian–Middle Palaeolithic. The remaining bones are distributed among the five Palaeolithic deposits and a single Chalcolithic deposit, at Los Millares, Almería (Table 5).

It is interesting to note that in the Palaeolithic deposit Cueva de la Carihuela (Piñar, Granada), Lumley (1969) mentioned an abundance of horse remains, although the results of Bouchud (1969) were different, possibly due to his dependence on photographs instead of the actual remains for that study. Samper (2010) studied the equids of the same archaeological site (NISP = 1118 isolated tooth fragments), and could assign 197 to *E. ferus* and 55 to *E. hydruntinus*. The rest of the bones are designated as *Equus* sp. due to the high degree of fragmentation. More recently Strani and DeMiguel (2023) studied a subset of these teeth (72 *E. ferus* and 13 *E. hydruntinus*) to look at diet based on microwear and found that they had included some browsing in their diet not too long before death, suggesting some level of flexibility in their diet. All the Palaeolithic archaeological sites with equids are in the drier eastern part of Andalusia (Fig. 2). The Neolithic and Chalcolithic have a large number of bones that have not been identified to species (Tables 6 and 7), apparently due to uncertainty regarding domestication status. By the Bronze Age almost all bones are identified to species as the domestic horse (Table 7).

The two asses, *E. asinus* and *E. hydruntinus*, are much rarer than the caballine species (Table 4). The wild European ass is identified primarily in the Paleolithic record. In addition to the

Table 5. Palaeolithic registers from Andalucia. Number of Equids identified in each level of each Palaeolithic site in Andalucia included in this study, as well as the total number of identified Class I and II ungulates and the percentage of ungulates identified that are equids. FE, *Equus ferus*; CA, *E. caballus*, HY, *E. hydrantinus*, AS, *E. asnus*, SP, *Equus sp*.

Province	Archaeological site	Culture-date	FE	CA	HY	AS	SP	Classes I and II	% Equids	Reference(s)
Almería	Cueva de Ambrosio	26 000–19 000 a BP	16	0	0	0	0	99	16.16	Ripoll, 1986; Jordá et al., 2012
		Middle Solutrens	147	0	0	0	0	1871	7.86	Yravedra, 2007
		Upper Solutrens	220	0	0	0	0	1229	17.90	
Córdoba	Sima de Abraham	40 000–20 000 a BP	0	0	0	0	2	67	2.99	Martínez et al., 2010
Granada	Cueva Horá	100 000–30 000 a BP	309	0	43	0	0	439	80.18	Martín-Penela, 1986
Granada	Cariguela	90 000–13 000 a BP	2	0	0	0	0	8	25.00	Bouchud, 1969* ; Villar, 1998
Granada	Cueva de los Ojos	Solutrens	0	*	0	0	0	0	–	Almohalla & Toro, 1985*
Málaga	Boquete de Zafarraya	42 000–34 000 a BP	7	0	6	0	3	3116	0.51	Barroso et al., 2003; 2006; Monclova et al., 2012
Málaga	Cueva de Nerja	20 000–17 500 a BP	0	0	0	0	3	1094	0.27	Riquelme et al., 2005-2006
Gibraltar	Devil's Tower	Mousteriens	3	0	0	0	0	40	7.50	Bate, 1928†
Gibraltar	Cueva de Gorham	26 070–24 010 a BP	4	0	0	0	0	331	1.21	Rodríguez-Vidal et al., 2010
		Mousteriens	12	0	0	0	0	769	1.56	Zeuner & Sutcliffe, 1964
		18 600–10 800 a BP	0	0	0	0	7	464	1.51	Finlayson et al., 2008; Rodríguez-Vidal et al., 2010; Riquelme et al., 2011
Total			913	0	104	0	15	10,637	9.70	

*These data are not complete; the analyses were carried out based on photos. Lumley (1969 _ remarked on the abundance of horses.
†These data are not complete.

Table 6. Neolithic registers from Andalucia. Number of equids identified in each level of each Neolithic site in Andalucia included in this study, as well as the total number of identified Class I and II ungulates and the percentage of ungulates identified that are equids. FE, Equus ferus; CA, E. caballus; HY, E. hydrantinus; AS, E. asnus; SP, Equus sp.

Province	Archaeological site	Culture date	FE	CA	HY	AS	SP	Classes I & II	% Equids	Reference(s)
Almería	Cerro de Los López	Late Neolithic	0	0	0	0	1	262	0.4	Riquelme, 2003
Cádiz	Cueva Parralejo	Early Neolithic	0	0	0	0	1	358	0.3	Morales & Riquelme, 2004
Cádiz	Cueva de la Dehesilla	Late Neolithic	0	0	0	0	1	219	0.5	Morales & Riquelme, 2004
Cádiz	Cueva Higueral de Valleja	Neolithic	0	19	0	3	0	283	7.8	Cáceres, 1997
Cádiz	El Retamar	5784–5773 BCE 5992–5780 BCE 5756–5754 BCE	0	0	0	0	18	279	6.5	Cáceres, 2002; Ramos et al., 2005
Granada	La Carigüela	Early Neolithic	0	0	0	0	4	76	5.3	Morales & Riquelme, 2004
		Middle Neolithic	0	0	0	0	1	156	0.6	
		Late Neolithic	0	0	0	0	1	105	1.0	
Granada	La Molaina	Middle Neolithic	0	0	0	0	1	803	0.1	Morales & Riquelme, 2004; Carrasco et al., 2011
Granada	Los Castillejos	5250–4900 BCE	0	0	0	0	3	1126	0.3	Morales & Riquelme, 2004,
		4900 BCE	0	0	0	0	1	1103	0.1	Cámara et al., 2005
		3100 BCE	0	0	0	0	30	1184	2.5	Ziegler, 1990
			0	0	0	0	16	1402	1.1	Morales & Riquelme, 2004; Cámara et al., 2005
			0	0	0	0	5	412	1.2	Uerpmann, 1990
Huelva	Papa Uvas	Late Neolithic–Chalcolithic 4350 BCE	0	0	0	0	4	401	1.0	Morales, 1985; Álvarez & Chaves, 1986; Mederos, 1996
		3033 BCE 3640 BCE	0	1	0	0	0	605	0.2	
Jaén	Polideportivo de Martos	Late Neolithic–Chalcolithic 3514–2911 BCE 3367–3108 BCE 3376–2878 BCE	0	0	0	0	14	1187	1.2	Riquelme et al., 2012; Afonso et al., 2014
Sevilla	Santiago Chica	6650 BCE 6040 BCE 5070 BCE	0	0	0	0	6	277	2.2	Mederos, 1996; Bernáldez-Sánchez, 2009
		5290 BCE 4350 BCE	0	0	0	0	3	51	5.9	
Total			0	20	0	3	110	10 289	1.3	

Table 7. Chalcolithic registers from Andalucia. Number of equids identified in each level of each Chalcolithic site in Andalucia included in this study, as well as the total number of identified Class I and II ungulates and the percentage of ungulates identified that are equids. FE, *Equus ferus*; CA, *E. caballus*, HY, *E. hydrantinus*, AS, *E. asnus*, SP, *Equus* sp.

Province	Archaeological site	Culture-date	FE	CA	HY	AS	SP	Classes I & II	% Equids	Reference(s)
Almería	Terrera Ventura	4700–4400 a BP	0	4	0	0	0	2710	0.15	Driesch and Morales, 1977; Crees and Turvey, 2014
Almería	Almizaraque	Chalcolithic	0	42	0	0	0	7109	0.59	Delibes de Castro et al., 1994
Almería	Los Millares	3095–2920 BCE 2890–2665 BCE 2590–2495 BCE 2900–2680 BCE	36	0	0	0	0	10 499	0.34	Navas et al., 2005
Cádiz	Cueva Higueral de Valleja	Chalcolithic	0	21	0	3	0	304	7.89	Cáceres, 1997
Granada	Los Castillejos	2550 BCE	0	0	0	0	36	1119	3.22	Riquelme, 1998; Cámara et al., 2005
		Chalcolithic	0	0	0	0	2	381	0.52	
		2000 BCE	0	0	0	0	4	916	0.44	
Granada	Cerro de la Virgen	Chalcolithic	0	14	0	0	0	5205	0.27	Driesch, 1972; Driesch 2000
Huelva	Cabezo Juré	4220 ± 120 a BP 4059 ± 120 a BP	0	0	0	0	58	4159	1.39	Nocete et al, 1999; Riquelme, 2004
		3980 ± 100 a BP 3880 ± 100 a BP 3870 ± 100 a BP 3850 ± 100 a BP 3830 ± 100 a BP 3568 ± 51 a BP	0	0	1	0	19	2592	0.77	Nocete et al., 1999
Huelva	Junta de los Ríos	2528 BCE 2525 BCE 2777 BCE 2707 BCE 2533 BCE	0	0	0	0	8	938	0.85	Abril et al., 2007; Nocete, 2008; Nocete et al., 2009
Jaén	Ciudad de la Justicia	Chalcolithic	0	0	0	0	9	831	1.08	Riquelme, 2010
Jaén	G. Triviño	Chalcolithic	0	0	0	0	3	904	0.33	Riquelme et al., 2012
Jaén	Tramo 3	Chalcolithic	0	0	0	0	11	2562	0.43	Riquelme et al., 2012
Jaén	Subestación	Chalcolithic	0	0	0	0	1	131	0.76	Riquelme et al., 2012
Jaén	Corte Inglés	Chalcolithic	0	0	0	0	1	157	0.64	Riquelme et al., 2012
Jaén	Los Pozos	Chalcolithic	0	1	0	0	0	178	0.56	Nocete, 1994
Jaén	Las Eras	3353 ± 103 BCE	0	0	0	0	88	2538	3.47	Riquelme, 2009
		Chalcolithic	0	0	0	0	61	1235	4.94	
		Chalcolithic	0	0	0	0	29	1098	2.64	
Málaga	Cueva del Toro	4120 ± 120 cal a BP	0	0	0	0	1	1		Watson et al., 2004
Málaga	El Silillo	3965 ± 40 a BP 3980 ± 40 a BP 3775 ± 40 a BP	0	0	0	0	1	80	1.25	Fernández et al., 2014
Sevilla	Amarguillo II	4070 ± 60 a BP 4030 ± 64 a BP	0	0	0	0	22	837	2.63	Cabrero et al., 2006
Sevilla	Cerro de la Cabeza	3530–2700 BCE 2880–1910 BCE	0	0	0	0	175	37355	0.47	Hain, 1982, Mederos, 1996
Sevilla	La Gallega	2480–2285 BCE	0	0	0	0	34	1424	2.39	Bernáldez-Sánchez et al., 2013; García Sanjuán et al., 2018
Sevilla	Parcela Municipal	3090–2465 BCE 2565–2195 BCE	0	0	0	0	2	288	0.69	Bernáldez-Sánchez et al., 2012; García Sanjuán et al., 2018
Sevilla	Cueva Antoniana	4765–4834 cal a BP	0	0	0	0	1	4	25.00	Mederos, 1996; Bernáldez-Sánchez, 2009
Sevilla	Gilena 89	Chalcolithic	0	0	0	0	1	6	16.67	Bernáldez-Sánchez, 2009
Total			36	82	1	3	567	85 561	0.81	

registers in our dataset, *E. hydruntinus* has been identified in the Palaeolithic deposit of the Cueva de la Carihuela (NISP = 55; Samper, 2010), but this site is not included in our analyses because the rest of the faunal data are not available. Two *E. hydruntinus* bones have been identified that are not from the Palaeolithic: one from the Chalcolithic site of Cabezo Juré in Huelva (Western Zone; Riquelme, 2004) and one in Terrera Ventura in Almería (Eastern Zone; Crees and Turvey, 2014; Driesch, 1972). The layer from Terrera Ventura has since been re-dated and shown to be Medieval, not Chalcolithic (Driesch, 2000). The bone identified as *E. hydruntinus* from Cabezo Juré is a phalange, and so we compared its measurements to known donkeys, mules and horses from archaeological sites, as well as modern horses (Fig. 6; Table S1), and found that its width/length ratio clusters it outside of the donkeys and within the mules. This suggests a much more recent mule, not a European wild ass, and could explain why it was difficult to identify. This brings the most recent confidently identified *E. hydruntinus* remains to the Palaeolithic.

The donkey is rare but reported in the Neolithic and Chalcolithic. Although the highest frequency is reported in the Neolithic, then declining in the Chalcolithic and Bronze Ages (Fisher's exact test, $P < 0.05$, considering two Chalcolithic *E. hydruntinus* as *E. asinus*), there is low taxonomic certainty

Table 8. Bronze Age registers from Andalucia. Number of Equids identified in each level of each Bronze Age site in Andalucia included in this study, as well as the total number of identified Class I and II ungulates and the percent of ungulates identified that are equids. FE, *Equus ferus*; CA, *E. caballus*, HY, *E. hydrantinus*, AS, *E. asnus*, SP, *Equus sp.*

Province	Archaeological site	Culture-datation	FE	CA	HY	AS	SP	Classes I & II	% Equids	Reference
Almería	Gatas	2,250-1,950 BCE1,950-1,700 BCE1,700-1,500 BCE	0	3	0	0	0	198	1.52	Montón, 1999
Almería	Fuente Álamo	2,200-1,950 BCE	0	10	0	0	0	5368	0.19	Manhart et al., 2000
		1,950-1,550 BCE	0	51	0	0	0	13,936	0.37	
		2,200-1,550 BCE	0	38	0	0	0	7402	0.51	
		1,550-1,350 BCE	0	50	0	0	0	3220	1.55	
Almería	Peñalosa	1,750 BCE	0	228	0	0	0	1190	19.16	Sanz and Morales, 2000
Córdoba	Torreparedones	EarlyBronze Age	0	0	0	0	1	25	4.00	Hamilton, 1999
		Late Bronze Age	0	0	0	0	2	18	11.11	
Granada	Loma de la Balunca	Bronze Age	0	4	0	0	0	547	0.73	Milz, 1986
Granada	Terrera del Reloj	Bronze Age	0	7	0	0	0	3127	0.22	Milz, 1986
Granada	Castellón Alto	Bronze Age	0	75	0	0	0	3331	2.25	Milz, 1986
Granada	Cerro de la Virgen	2,000-1,600 BCE	0	1061	0	0	0	21,217	5.00	Driesch, 1972
		1,600-1,200 BCE	0	519	0	0	0	5851	8.87	
Granada	Cerro de la Encina	EarlyBronze Age	0	10	0	0	0	808	1.24	Friesch, 1987
		MiddleBronze Age	0	145	0	0	0	3125	4.64	
		Late Bronze Age	0	73	0	0	0	175	41.71	
		Late Bronze Age	0	71	0	0	0	1565	4.54	
Jaén	Las Eras	1,831±48 BCE	0	0	0	0	9	1185	0.76	Riquelme, 2009
Málaga	Acinipo	Late Bronze Age	0	2	0	0	0	5608	0.04	Riquelme, 1994
			0	**2347**	**0**	**0**	**12**	**77,896**	**3.03**	

associated with the Neolithic specimens. Regardless, the number of records is very low, so it is probably best to simply consider them present at a very low frequency.

Discussion

Different species of equids are found in the archaeological record of Iberia through the last 45 000 years, both in cave art representations and in the zooarchaeological register (Bernáldez-Sánchez and García-Viñas, 2019): *Equus ferus*, the wild horse which was later replaced by the domestic horse *Equus caballus*; the domestic donkey *Equus asinus*; and the extinct European wild ass *Equus hydruntinus*. Although the larger horses (*E. ferus* and *E. caballus*) can generally be morphologically distinguished from the smaller asses (*E. hydruntinus* and *E. asinus*), given intraspecific variation and the possibility of hybrids (mules), identification can be difficult (Granado et al., 2020). The most difficult pair to distinguish are the wild horse (*E. ferus*) and its domestic descendant (*E. caballus*), a distinction further complicated by their presumed ability to hybridize (Der Sarkissian et al., 2015) and a change in their morphology through time (Fig. 6).

On the Iberian Peninsula, the first clearly accepted domesticated horses are found within the Bronze Age (Liesau, 2005; Martín et al., 2016). This is well after domestic horses have been documented in other parts of Eurasia (Olsen, 2000; Outram et al., 2009; Gaunitz et al., 2018). The high level of maternally inherited genetic diversity documented in modern horses (Vilà et al., 2001; Cieslak et al., 2010) suggests that horses, or at least mares, from many geographical localities may have participated in the domestication process, either through independent domestication or through the crossing of local, wild mares with domestic (imported) stallions. There is some evidence that at least some Iberian mares were included (Lira et al., 2010; Leonardi et al., 2018). These two alternatives, both compatible with the genetic data, mirror the wider debate between indigenist and exogenous views of Iberian prehistory, the importance of mobility vs. alterity (Lillios 2020).

In the Chalcolithic when there certainly were domestic horses in Eurasia, but it is not clear if they were in the Iberian Peninsula or not, remains are rarely identified to species (Table 4). This could reflect their in-between status. They could have been lightly controlled by humans in order to support the population primarily for hunting – as may have taken place in the early part of the domestication period in other locations (Librado et al., 2021). Alternatively, it may reflect a mix of domesticated and wild individuals. It could also simply reflect a reluctance to make a determination when the morphology is so similar. Other types of data could help disentangle these alternative hypotheses, similar to how protein analyses of residues on pottery in Kazakhstan demonstrated the domesticated status of those horses (Outram et al. 2012). Since wild Iberian horses were genetically distinct from other Eurasian horses (Cieslak et al., 2010), the identification of Eurasian variants would demonstrate that the presence of domestic animals (although the absence of Eurasian variants would not prove that they were wild, because if there had been local domestication, those animals would have had local genetic lineage). The change from wild to domestic status could also be reflected in the diet of the individuals, which could be evaluated with stable isotopes (BurnikŠturm et al., 2017), microwear patterns (Strani and DeMiguel 2023), or in kill-off patterns determined through analysis of the sex and age structure of large deposits (Martín et al., 2016).

Domestic horses are a cultural artefact, but the keeping of horses may have been impacted by environmental change as well as cultural change. The data presented here show that the frequency of horses was associated with climatic conditions, such that there were more horses east of the Guadalquivir River in Andalucia during the Bronze Age, associated with a drier climate more favourable to grasslands (Lillios et al., 2016; Bini et al., 2019). This parallels the larger

Figure 6. Morphological measurements of equid first phalanges, with length (GL in mm) on the *y*-axis and width (SD in mm) on the *x*-axis. Domestic donkeys are in the bottom left, ancient horses are shifted to the right from mules in the centre of the graph, and modern horses are the largest individuals in the top right of the graph. [Color figure can be viewed at wileyonlinelibrary.com]

European pattern (Sommer et al., 2011; Leonardi et al., 2018). Human activity can also cause changes in the environment, such as through deforestation, which may also increase the extent of grasslands and facilitate the maintenance of equids. There is evidence of patchy anthropogenic deforestation in the Iberian peninsula during the Holocene (García-Ruiz et al. 2016). In this specific case, the observed increase in the frequency of equid records in the Bronze Age corresponds in time with a change to a strongly arid period (Bond event 3; Bond et al., 2001; López-Sáez et al., 2018). Although these horses were clearly domestic and keeping domestic horses is a cultural activity, the number of horses was still strongly influenced by the climate (Blanco-González et al., 2018).

The wild European ass was present across southern Europe and into western Asia in the late Pleistocene (*E. hydruntinus*; Orlando et al., 2006), but this was not the ancestor of the currently present domestic donkey (Beja-Pereira et al., 2004; Vilà et al., 2006). Although this species was quite geographically widespread, in any given site it is generally rare (e.g. Table 5). The low frequency of these remains complicates the accurate identification of their fine-scale distribution, and eventual extinction. The timing of the extinction of the European wild ass on the Iberian peninsula is debated, and some Chalcolithic osteological remains have been assigned to this species (Table 7), although habitat reconstructions suggest an earlier extinction (Crees and Turvey, 2014). The morphological data presented here also support the earlier extinction of this lineage (Fig. 6).

Just as the European wild ass is much less frequent in the early zooarchaeological record than the wild horse, the domestic donkey is also much less frequent than the domestic horse in more recent registers (e.g. Table 7). Just as rarity complicates identification of the time of extinction of the European wild ass, it also complicates identification of the time of arrival of this domestic species to the region. Although the ambiguous morphology may obscure identification in some cases, since the domestic donkey is not the descendant of the local wild ass, they can be clearly differentiated genetically (Cardoso et al., 2013). The earliest domestic donkey on the Iberian peninsula, from about 4 ka BP, was identified based on genetic analyses (Cardoso et al., 2013). It seems probable that the domestic donkey did not coexist with the European wild ass in Iberia.

One of the factors that obscures the morphological differentiation of horses and donkeys is their ability to hybridize and form morphologically intermediate mules. Mules can be confused with horses (Granado et al., 2020), which were generally smaller in the past than they are today (Fig. 6). The correct identification of mules is important in order to better understand the associated human societies. There are some real advantages to having strong, good tempered mules as opposed to more fragile horses or more 'grumpy' donkeys. However, they are also costly. In order to have mules it is necessary to maintain populations of both horse and donkey, since the mules themselves are sterile. In other parts of Europe, the early presence of mules has been associated with Romans (Granado et al., 2020), compatible with the Andalucian record (Fig. 6; Table 7).

Conclusion

This compilation and analysis of data furthers our understanding of how and when populations of equids changed through time in Andalucia, the southern part of the Iberian Peninsula, and also reveals some gaps in our knowledge. By putting these data together, a significant geographical bias in the available data becomes apparent with a lack of information from the more mountainous regions and the Guadalquivir basin (Fig. 1), perhaps deriving from the tendency of archaeozoological studies to be undertaken in areas near to specialists' research institutions. These data also highlight the low frequency of zooarchaeological analyses of archaeological sites (Fig. 1). Depending on whether material was saved from excavations and deposited in public collections, this gap could be reduced. The lack of sites from around 13.7 to 8 ka BP, such as the gap at the Copper to Bronze Age in the low-elevation regions of the Guadalquivir basin, could represent an actual shift in the local distribution of people (López-Sáez et al., 2018), or a lack of data. Conclusively confirming a true negative (that the population actually did decline or move away from the area) requires much more effort than disproving an absence. The combination of multiple lines of evidence, such as focused searching of sites likely to have humans based on environmental reconstructions and indirect measures of human presence such as changes in fire regime or pollen as recorded in regional palynological records, may make this work more efficient. The results of this study paint a clearer picture of an early (end Paleolithic) extinction of the European wild ass in the region, and also the earlier (Neolithic) arrival of domestic donkeys and breeding of mules. Determining the timing (Chalcolithic or Bronze Age) and origin (local and/or imported) of the first domestic horses in Andalucia requires more work, but this study illuminates the path forward through this analysis of available data and identification of important gaps.

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Data availability statement

The data in our paper were derived from many papers, reports and book chapters which are all listed in the Mosaico database and Table 1. The derived data (number of equids and other large ungulates) are provide in the Tables. Morphological data are available in Supplementary Table S1.

Supporting information

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Supplementary Table S1. Measurements of 1st falange of equids from different species and time periods from Andalucia illustrated in Figure 6. Length (GL) and width (SD) of phalanges are in mm.

Abbreviations. ka BP, thousands of years before present; kyrs, thousands of years; Mosaico, Andalusian Historical Heritage Information System (Sistema de Información para la Gestión del Patrimonio Cultural en Andalucía); NISP, minimum number of specimens.

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