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A non-linear prediction model for ageing foetal and neonatal sheep reveals basic issues in early neolithic husbandry

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ABSTRACT

Traditional methods for estimating age-at-death of caprines are based on dental and epiphyseal fusion data and known to produce rather wide age intervals. In order to better interpret prenatal to early infantile mortality of sheep in prehistoric assemblages more precise age predictions are needed. We address this issue using a Generalized Additive Model (GAM) developed on humerus measurements of unborn and very young sheep of known age housed in modern collections. We then verify the resulting prediction model with the aid of a pregnant ewe and her foetus (*Ovis aries*) excavated in the Ptolemaic-Roman animal cemetery at Syene (modern Aswan, Egypt). Her condition illustrates that both the mother and her mature foetus must have died during birthing. Subsequently, we apply the model to humeri of very young archaeological sheep (*Ovis orientalis/O. aries*) unearthed at early Neolithic Aşıklı Höyük (Central Turkey). Both study cases underscore the practicality of our approach whilst illustrating the cultural and historical importance of precise age determinations in foetal, newborn and infantile sheep. Finally, we discuss the possible causes for foetal and neonatal mortality in sheep at Aşıklı Höyük.

1. Introduction

Traditional archaeozoological methods for estimating age-at-death in faunal assemblages largely rely on dental (e.g., Deniz and Payne, 1982; Greenfield and Arnold, 2008; Grant, 1982; Payne, 1973) and epiphyseal fusion data (e.g., Popkin et al., 2012; Silver, 1969; Zeder, 2006), more seldom on bone morphology and texture (e.g., Amorosi, 1989). The resulting kill-off patterns and demographic profiles are widely used for investigating subsistence strategies and economic decision-making (e.g., Payne, 1973; Vigne and Helmer, 2007), cultural and ritual practices (e.g., Pöllath and Peters, 2011) or the initial phases of the domestication process (e.g., Peters et al., 2014; Zeder, 2005). For these purposes, methods traditionally used by zooarchaeologists are acceptable despite the comparably rough prediction intervals provided by them. However, when investigating an assemblage of foetuses and very young animals until the age of about six months and the possible causes of death it is crucial to know if these animals were aborted, stillborn, died shortly after birth or during the weaning period. In such cases fine-tuned age predictions are highly desirable. In present-day recordings, the earliest dental stage, Payne's (1973) stage A (the lower fourth deciduous premolar (Pd₄) 'not yet erupted' to 'just worn'), comprises all animals until c. two months of age. Even if this stage can be narrowed down to six weeks after birth as proposed by Jones (2006), the large majority of very young animals would not further be differentiated since still classified into a single stage. Age intervals based on epiphyseal fusion are even wider than those based on dental eruption and wear. The

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earliest long bone fusion stage in sheep defined by the complete fusion of the proximal radius ranges from the animal's birth to three months of age for the Rasa Aragonesa sheep of northern Spain (García-González, 1981) and up to between six and eight months based on historical data (Silver, 1969; see also the summary in Zeder, 2006).

In veterinary gynaecology and obstetrics, body measurements taken postmortem or on X-ray and ultrasound images are employed in order to estimate the stage of pregnancy and monitor foetal development in ewes (e.g., Ahmed, 2008; Godfrey et al., 2010; Greenwood et al., 2002; Habermehl, 1975; Santucci et al., 1993). These also include length measurements of limb bones (Ahmed, 2008; Greenwood et al., 2002; Habermehl, 1975; McDonald et al., 1977; Santucci et al., 1993). Based on diaphysis length measurements, the following authors developed equations allowing them to calculate the age of foetal sheep: Richardson et al. (1976) for the radius and tibia, Santucci et al. (1993) for the metatarsal and Greenwood et al. (2002) for the metacarpal. McDonald et al. (1977) combined length and breadth measurements with foetal weights to study the development in multiple foetus pregnancies. Other studies list length measurements of the diaphyses for major limb bones of foetuses aged between 45 and 131 days (Rajtová in Habermehl, 1975) and for the forelimb between 7 and 15 weeks after gestation (Ahmed, 2008).

Bone measurements are rarely used in archaeozoology to age foetal or infantile animal bones. One exception is Prummel (1988), who reviewed the regression equations developed by veterinarians for the four main farm animals, cattle, horse, sheep and pig. In the other two articles of the series, this author also gives an overview of the prenatal development of the skeleton of these four species and a guide to the taxonomic identification of foetal bones. Unfortunately, no differentiation between foetal and postnatal stages is provided (Prummel, 1987a, b). Another exception is Gillis et al. (2013), who for the first time based linear age prediction models for very young cattle on measurements. They demonstrated that breadth and depth measurements are particularly useful and reliable for some elements with up to 100% of the values within the 95% confidence interval (Gillis et al, 2013, Table 3).

Martín and García-González (2015) applied the age determination equations proposed by Richardson et al. (1976) and Santucci et al. (1993) to the radius, tibia and metatarsal but developed in addition osteomorphological criteria to distinguish foetal from neonatal sheep based on a series of foetal to adult skeletons of a single Spanish breed, the Rasa Aragonesa. These authors concluded that morphological criteria are more reliable than length measurements to perform such distinction.

Arguably, precise ageing of very young sheep from archaeological sites is of interest when addressing husbandry practices and health status in past livestock populations. An interesting case study is offered by the caprine remains excavated at early Neolithic Aşıklı Höyük (Central Turkey) dated between c. 8350 and 7300 BCE. In a first attempt we considered the morphological criteria as presented by Martín and García-González (2015). Unfortunately, many of these could not be applied since the relevant parts of the bones were not well enough preserved. Additionally, some features, e.g., in the humerus (Martín and García--González, 2015) are located on the distal epiphysis, which are very rare in our archaeological assemblage. Our findings agree with the results of Martín and García-González (2015) stating that length measurements are not helpful for age predictions when dealing with archaeological specimens, simply because complete bones are rarely preserved. As such, the aforementioned authors also consider the mid-shaft depth of a long bone (also termed the anterior-posterior breadth at mid-shaft), but with the Aşıklı finds this measurement can rarely be taken due to their pronounced fragmentation. Therefore, breadth measurements of the proximal and distal ends of the diaphyses for unfused bones and of the epiphyses in the case of fusing or fused bones seem to be the more appropriate option for archaeological materials. Additionally, early fusing elements are generally better ossified even in foetal and neonatal specimens, while diaphyses of late fusing elements are rarely preserved

sufficiently well to be measured, which applies to the corresponding epiphyses even more.

In the early Neolithic assemblage from Aşıklı Höyük (AH), the distal diaphysis of the humerus provided the largest usable dataset (n = 43; for comparison radius: n = 22). Since the distal breadth of the humerus was also among the most reliable measurements in the study of very young cattle by Gillis et al. (2013), our study develops a prediction model for the humerus of foetal and young lambs using modern reference material of known age and, in the case of foetal animals, for which the exact age was not recorded, calculated ages based on body weight (for the method see below). The outcome will be tested with a unique case of a mature foetus deposited in Ptolemaic-Roman Syene (present-day Aswan, South Egypt) and finally applied to the assemblage of very young animals from Aşıklı Höyük mentioned earlier. This study concludes by elucidating the causes of mortality in modern foetal and young lambs in order to better understand the problems faced by sheep breeders during the process of early caprine management and domestication at Aşıklı Höyük.

2. Gestation period and skeletal development in sheep

The gestation period of sheep is usually given with a range of 141–150 days on average (Diggins and Bundy, 1958; Geiger et al., 2018; Grunert, 1993; Haring, 1975). While this is based on modern breeds from temperate climates, gestation periods tend to be generally longer in indigenous sheep from subtropical and tropical regions (Legel, 1990). For example, the overall mean for three fat-tailed sheep breeds kept in three different production systems (nomadic, sedentary, transhumant) in the semi-arid and subtropical central valley of Pakistan is given as 160 days (Ibrahim et al., 2011). In former times, variation in gestation periods also seems to have been larger, i.e. between 136 and 160 days, as suggested by a study considering 16 breeds (Golf, 1933). The gestation period for feral Soay sheep, living in the extreme environment of the St Kilda archipelago, was found to be 148-155 days with a mean of 151.15 days (Jewell and Grubb, 1974). The same study also states that pregnancies last longer in ewes of late maturing breeds. In older ewes, gestation periods may also be longer than in young ewes (Haring, 1975).

Gestation time for wild sheep species is also decidedly longer as compared to improved domestic breeds mentioned above (see the overview in Geiger et al., 2018). Both the longest gestation period and the largest range for all wild sheep species has been reported in the presumed ancestor of the domestic sheep, the Asiatic mouflon (*Ovis orientalis*), with 150–210 days (Castelló, 2016). The duration seems somewhat exaggerated, though, since for most other related *Ovis* (sub-) species of the same region a range of 150–160 days is given by the same author, with the exception of the European mouflon (*Ovis aries musimon*), for which also a period of 150–210 days is stated. This contradicts most other published data on European mouflons mentioning gestation periods lasting 147–160 days (Pfeffer, 1967; Röhrs, 1986; Türcke and Tomiczek, 1982).

Regarding skeletal development of foetal sheep, the primary ossification centre in the humerus, which is located in the diaphysis, appears around day 40 after conception (Ahmed, 2008: 46 days; Harris, 1957: 42 days; Rajtová, 1972: 37 days). The secondary ossification centres in the different parts of the epiphyses begin to ossify from day 104 onwards (Harris, 1957). Two days before birth the diaphysis and the epiphyses are already well ossified (Rajtová, 1972). The growth of the humerus is fast in the first five weeks after birth and again between day 130 and 150 (Rajtová, 1974).

The dates proposed for epiphyseal fusion in limb bones vary between authors (Zeder, 2006: Fig. 4). For the distal humerus, the age of synostosis between the distal trochlea and the diaphysis ranges between 2 to 4 months (García-González, 1981) and 10 months (Silver, 1969). This large variation can be partly explained by the different breeds used for generating this kind of data. Another reason is that some authors consider the moment when fusion starts, others when it is completed; still others refer to the complete period of fusion. An example for the

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latter is Rajtová (1974), who states that fusion of the distal humerus starts at 3-4 months and is finished at 9 months in Slovenské merino sheep. García-González (1981) studied a series of skeletons of the Spanish breed Rasa Aragonesa and defined that an epiphysis is fused when the epiphysis and the diaphysis do not separate even after boiling the bones for a few hours. During re-analysis of the same skeletons for this study, we observed that distal humeri start fusing at an age of 2 months and that the process lasts several months. Variation is considerable, though, since in a female individual aged 6 months the epicondylar sutures were still not fully closed, while in a male specimen of the same age no such sutures were visible anymore. This implies that in this breed, the fusion lasts four months in total and takes place between c. 2 and 6 months of age. In this light, it seems that the dates published by Silver (1969) refer to the end of the fusion process. In their study on unimproved Shetland sheep, Popkin et al. (2012) found that more than a quarter of the humeri were fully fused distally while the rest still had visible fusion lines at the age of seven months.

3. Material

3.1. Definition of age groups

The age groups used in this study are: foetal = four weeks after conception until birth; perinatal = around birth, i.e., *c*. one week before and after birth; neonatal = from birth until four weeks of age, when lambs start to take solid food; infantile = from four weeks to five months (i.e., c. 42 weeks after conception) when the natural weaning process ends (Arnold et al., 1979); juvenile and subadult = between five months and four years; adult = four years and older.

3.2. Modern reference collections

The data set compiled in the context of this study is based on the analysis of 140 modern sheep specimens from the following collections: Natural History Museum (NHM, London, UK), Historic England (HE, Portsmouth, UK), Field Museum of Natural History (FMNH, Chicago, USA), Instituto Pirenaico de Ecología (IPE, Jaca, Spain), Laboratório de Arqueosciências (LARC, Lisboa, Portugal), Museum für Haustierkunde "Julius Kühn" (MfH, Halle/Saale, Germany) and Staatssammlung für Anthropologie und Paläoanatomie, München (SAPM, Munich, Germany) (Table 1; Table S1). We initially included a variety of breeds and two wild forms of sheep primarily because it is necessary to base statistical analyses on the largest possible database. Indeed, as stated by other authors (Gillis et al., 2013; Prummel, 1987a), analyses based on

Table 1

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single breeds run the risk to produce narrow age estimates so that the predicted ages for prehistoric sheep, which possibly deviate in terms of body conformation and physiology from that of any specific modern breed, would be misleading. Since the methods include two main steps, i.e., one establishing body conformation types and another developing the prediction model, we recorded not only data for young animals for the second step but also juvenile to adult animals for the first step. Altogether we gathered the data of 2 foetal, 46 neonatal to infantile, 25 juvenile to subadult and 28 adult animals from modern reference collections (Table S1).

3.3. Archaeological material

The incentive to detail the timing of age-at-death of very young caprines came up whilst analyzing a huge assemblage of sheep and goat remains from Aceramic Neolithic Aşıklı Höyük, Turkey (Table 1; Fig. 1). This site is the largest and best-studied settlement in central Anatolia dating to the initial phase of Neolithisation (Özbaşaran, 2012; Özbaşaran and Duru, 2018; Özbaşaran et al., 2018). Continuously inhabited from c. 8350 BCE until c. 7300 BCE, this site offers a wealth of data on architecture, material culture, human and animal diet, vegetation, subsistence strategies, and on the development of crop farming and animal husbandry, among others (for an overview see Özbaşaran et al., 2018). While hunting was still important for the subsistence of the inhabitants at the beginning of site occupation (Level 5), the management of caprines gained in importance from Level 4 (8350-8050 BCE) onwards, with sheep being the most important livestock species (Buitenhuis et al., 2018; Peters et al., 2018; Stiner et al., 2014, 2018). Thick layers of animal dung found inside the settlement indicate that caprines were penned for longer periods in or between the houses (Mentzer, 2018). Based on the development of the architecture and the structure of the settlement, the archaeological levels can be grouped broadly into three horizons, i.e. early [Levels 5-3], middle [Levels 2J-2D] and late [Levels 2C-2A] occupation. Almost the same numbers of specimens come from the middle (n = 18) and late horizons (n = 19) while one specimen dates to the early horizon and five specimens are unphased (Tab. S2). The scarcity of bones from the early levels is arbitrary owing to the fact that the earlier levels could not be included in the analyses yet. While the majority of bones from the middle and late levels belong to managed sheep (Buitenhuis et al., 2018), we consider bones of foetal to infantile animals to be almost exclusively being the offspring of those managed sheep since already the ewes were obviously kept confined within the settlement.

While bone preservation at Aşıklı Höyük is excellent overall, bones of

Modern	Breed	n=	Age	Analysis	Data acquisition
	Asiatic mouflon	female: 8; male: 8	adult	conformation type	N.P.
	European mouflon	female: 4; male: 4	adult	conformation type	Hijlke Buitenhuis
	Cameroon	female: 1; male: 1	adult	conformation type	N.P.
	Heidschnucke	female: 3; male: 1	subadult, adult	conformation type	N.P.
	Karakul	female: 3; male: 3	adult	conformation type	Hijlke Buitenhuis
	Leine	female: 3; male: 2	adult	conformation type	Hijlke Buitenhuis
	Manx	female: 1	adult	conformation type	N.P.
	Merina Branca, Merina Preta	female: 21; male: 5	adult	conformation type	Simon Davis
	Rasa aragonesa	female: 3; male: 2	adult	conformation type	N.P.
	Rhön	female: 3; male: 2	subadult, adult	conformation type	Hijlke Buitenhuis
	Rouge du Roussillon	female: 1; male: 1	subadult, adult	conformation type	N.P.
	Skudde	female: 1	adult	conformation type	Hijlke Buitenhuis
	Soay	female: 5; male: 6	adult	conformation type	N.P.
	Rasa aragonesa	26	foetal to infantile	conformation type, model	N.P.
	Welsh mountain	4	infantile	model	N.P.
Archaeological	Site	n=	Age	Analysis	
	Aşıklı Höyük	833	adult	conformation type	N.P., J.P., Hijlke Buitenhuis
		43	foetal to infantile	age prediction	N.P.
	Syene	32	adult	conformation type	U.M.
		1	perinatal	age prediction	U.M.



Fig. 1. Map showing the location of the archaeological sites of Aşıklı Höyük, Turkey, and Syene, Egypt.

young animals certainly witnessed greater losses also at this site since they are less well-ossified and therefore generally more prone to damages. These losses are, however, impossible to quantify. We excluded all specimens with damages to the distal end affecting the measurement of the Bd(Dia). At least nine specimens, which judging from their appearance most likely would fall into the foetal or newborn age classes, had to be omitted from the analyses due to damages.

In very young caprines, taxonomic identification to the species level is difficult and rarely possible, especially when dealing with fragmented archaeological specimens. In the humerus assemblage studied, we could assign only very few specimens to either sheep or goat. The remaining specimens were classified as unidentified caprines. However, sheep clearly outnumber goats throughout site occupation at Aşıklı Höyük, amounting to 80% of the taxonomically identified caprines. We can therefore safely assume that the vast majority of these very young caprines represent sheep as well. Moreover, since in *Ovis* and *Capra* foetal to infantile growth is rather similar (Sivachelvan et al., 1996), an occasional goat bone will not substantially distort the results presented below. Consequently, only those humeri that had been securely identified as pertaining to *Capra* were excluded. As a result a total of 43 unfused humerus remains were available for analysis (Tab. S2). Since these come mostly from different contexts in different layers and squares the risk of including two humeri from one individual is small. The few specimens from the same context included in our analysis are either from the same body side or have rather different measurements and are therefore quite certainly from different individuals.

To test the suitability of our novel approach, we also considered a particular find situation in the Ptolemaic-early Roman animal necropolis at Syene/Upper Egypt (first half of the 2nd cent. BCE – end of the 1st cent. CE) as test case (Fig. 1 Map; Table 1, Table S2; Hepa et al., 2018; Mutze et al., 2021; von Pilgrim and Müller, 2013). One of the pits contained a ewe with her foetus still *in situ* (Fig. 2). Because the ewe had a deformed hipbone due to a healed fracture causing obstruction of the birth canal, the foetus got stuck during parturition, ultimately leading to the death of mother and offspring. Here we have a quite unique archaeological situation allowing us to determine the age-at-death of the foetus to the very day of birth. Even if the ewe may have survived somewhat longer, the foetus likely died rather quickly in the birth canal.

4. Methods

4.1. Species identification

Species identification of *Ovis* and *Capra* is based on Boessneck et al. (1964) and Zeder and Lapham (2010). The criteria used for humeri of foetal and infantile animals were mainly the position of the *foramen nutricium*, the shape of the *fossa olecrani* as well as the shape and position of the *epicondylus lateralis* (Boessneck et al., 1964: 65–66; Fig. 27).

4.2. Data recording and treatment

For the modern reference specimens, we noted the fusion status and measurements for all limb bones as well as dental data. We recorded the osteometric data following the protocol of Gillis et al. (2013), with minor differences in the naming of the measurements (e.g., Gillis' Bdunf = Bd(Dia), Bdepi = Bd(Epi)). In this study, we will focus on the breadth of the distal humerus, more precisely Bd(Dia) for unfused specimens and Bd for fused specimens), simply for the reason that at Aşıklı Höyük, only the dataset for the humerus proved large enough to perform this kind of analysis (Table S2; Fig. 3).

We considered specimens for which the age-at-death was known and two foetal animals for model development. For the latter two in the IPE collection (IPE 200a, IPE 200b), Martín and García-González (2015) calculated the gestation age based on body weight applying the equation given by Huggett and Widdas, 1951, which we adopted. The method of documenting the ages of animals varies between institutions. For foetuses, for instance, ages are usually given in days, while for lambs this is rarely the case, with the exception of the sheep curated in the collections of Historic England. Elsewhere the ages of sheep had been recorded in weeks, months and years. Whereas time windows in the order of one month are too coarse for foetuses and age-at-death expressed in days too fine-tuned for infantile animals, we decided to develop our model based on the age in weeks after conception for all modern individuals and set the duration of gestation to 22 weeks. Our approach would also account for the noise induced by the differences in gestation times reported in 'primitive' prehistoric sheep, historic unimproved lineages and modern improved breeds, for old and young ewes or for wild and domestic sheep (see above section 2). In graphs where the inclusion of adult animals was necessary, their maximum age was set to 230 weeks, i.e. 4 years, even if their true age was above this mark. This is because detailed profiles of animals above 4 years of age was considered unimportant for our purpose. The equation by Huggett and Widdas (1951) was used to confirm that two stillborn individuals in the HE collection (HE 4028, HE 4029) corresponded to fully mature foetuses.

We also recorded the sex of the animals but did not include this in the analyses since sexes are not distributed evenly over the age range. Additionally, since the data is composed of a mixture of breeds and given



Fig. 2. Photograph of a burial of a ewe and her foetus at Syene. Skeleton of the ewe outlined in black, the bones of the lamb in orange and its body in red. By courtesy of the Schweizerisches Institut für Ägyptische Bauforschung und Altertumskunde in Kairo (11/13, Sh. el-Shaer Aziz Abaza. Cairo 11211 (Zamalek), Egypt). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



Fig. 3. Measurements defined on (a) the distal end of the diaphysis of unfused humeri and (b) the distal articulation of fused humeri.

that in domestic sheep sexual size dimorphism is relatively small (Polák and Frynta, 2009), possible differences in growth and size between sexes would be very blurred with the data at hand. As outlined above (see section 2), published fusion dates for the distal humerus range between 2 and 10 months depending on the mode they were recorded and the breed on which the study was based. Well aware of this range of variation, we decided to set the fusion of the distal end to 6 months after birth, which corresponds to 46 weeks after conception. In the following, this value will serve as a baseline.

4.3. Classification of modern sheep breeds and archaeological populations

On first graphical inspection (Fig. S1), the broad range of the data becomes obvious. It is caused by the inclusion of data obtained from small-sized to very large and/or heavy sheep breeds in the reference collections. Not only does this make a grouping of the various breeds according to their physical appearance necessary, but equally important is that separate prediction models must be developed for each group. For the breeds in our dataset, published data on body weight and withers height were listed and used to classify them into conformation groups

Fig. 4. Diagram showing the conformation groups based on the weight and the height at the withers of different sheep populations; (1) Cameroon, (2) Skudde, (3) Soay, (4) Rasa Aragonesa, (5) Karakul, (6) Welsh Mountain, (7) Rouge du Roussillon, (8) Rhön, (9) Leine, (10) Merino meat breed, (11) German blackhead, (12) European mouflon, (13) Asiatic mouflon (data and references see Table #2).

(Table 2; Fig. 4).

In a second step, the two archaeological sheep populations were allocated to the respective conformation group. For this, the breadth of the trochlea humeri (BT) of adult specimens from Aşıklı Höyük and Syene were graphically compared with those from the conformation groups. BT was chosen for this analysis because archaeological humeri are often damaged so that the distal breadth (Bd) cannot be measured in sufficient numbers, while the BT is still measureable even in many of the damaged specimens. As an early fusing element post-fusional growth affects the breadth measurements of the humerus particularly in male animals (Davis, 2000; Popkin et al., 2012). This becomes obvious in the wide spread of the Bd measurements of adult sheep in the upper part of Fig. S1. Preferring BT over Bd has the additional advantage that the first seems to be less affected by post-fusion growth, which mainly occurs on the medial and lateral condyles and less at the trochlea (Kazantzis and Albarella, 2016). For Fig. 5, the data listed in Table S1 were complemented with data of adult Karakul, Rhön, Leine sheep and European

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Table 2

Characteristics of modern sheep breeds.

Туре	Breed	Weight [kg]		Withers height [cm], Average	Reference	
		females	males			
Light	Soay	24–28	30–40	48.8	Sambraus (1994)	
	Cameroon	30-40	40–50	52.5	Bayerische Landesanstalt für Landwirtschaft (nd)	
	Skudde	40-45	50-55	53.8	Sambraus (1994)	
Medium	Rasa Aragonesa	35-50	45–70	64.5	García-González (1987)	
	Karakul	40-50	60–70	67.5	Sambraus (1994)	
	Welsh Mountain	50-60	70-80	67.5	Sambraus (1994)	
	Rouge du Roussillon	55-65	75–100	71.3	Brooke and Ryder (1978)	
	Rhön	55-65	70–90	74.0	Sambraus (1994)	
Heavy	Leine	70-80	100-120	77.5	Sambraus (1994)	
	German blackhead	70–90	100-130	81.3	Sambraus (1994)	
	Merino (meat)	75-85	120-140	82.5	Sambraus (1994)	
Wild	European mouflon	25-35	35–55	72.5	Barbato (2016)	
	Asiatic mouflon	35–45	55–67	87.0	Groves and Leslie (2011)	

mouflons housed in the MfH, Halle (data by courtesy of Hijlke Buitenhuis), and of Portuguese Merino sheep housed in the LARC, Lisboa (data courtesy of Simon Davis).

4.4. Non-linear GAM model

Our first graphical data exploration revealed a non-linear pattern (Fig. S1). This was to be expected since bone growth – like growth in many organisms in general – is non-linear and usually described most accurately as a sigmoid curve (e.g., Zullinger et al., 1984). Growth curves are most often modelled using non-linear functions such as the Richards, Gompertz or the logistic functions (e.g., Forsyth et al., 2016; Tjørve and Tjørve, 2017; Zullinger et al., 1984). We chose Generalized Additive Models (Hastie and Tibshirani, 1986, 1990) to capture the non-linearity of this relationship. Key advantage of GAM is the flexibility

for modelling not only non-linear relationships such as bone growth, but also to include linear and binary covariates into the model, such as nutrition plane and sex for larger datasets. The underlying model can be written as:

$$y_i = \alpha + f(x_i) + \varepsilon_i \tag{1}$$

where y_i is the response variable *age* for the *i*-th observation expressed in "weeks after conception", α is the intercept, which is in our case the mean age of the population, x_i is the *distal breadth of the diaphysis of the humerus*, f(.) is a smooth function of the covariate and ε_i is the *error term* of the model, with a mean equal to 0.

This model (1) allows for a rather flexible specification of the response *age* on the covariate *distal breadth*, by specifying the model in terms of "smooth functions". The smooth functions in GAMs are constructed as penalized thin plate regression splines and their optimal



Humerus, BT [mm]

Fig. 5. Classification of archaeological humeri based on the Breadth of the Trochlea (BT).

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shape is estimated by minimizing the general cross validation (GCV) criterion (for more details see Wood, 2017). In order to validate the model, we calculate the Root Mean Squared Error (RMSE). Subsequently the model residuals were graphically inspected and tested for assumptions of homogeneity of variance and normality (Zuur, 2012). Based on this model, we then predicted the age-at-death for the archaeological humeri from Aşıklı Höyük and Syene.

4.5. Chi-squared test for independence

In order to test whether pre- and postnatal lamb mortality at AH changed over time we conducted a chi-squared test for independence between the middle and the late horizon. The only case pertaining to the early horizon at AH was added to the middle horizon (Table S2). Lamb mortality was divided into two groups: a group containing cases occurring during late pregnancy until birth and a second group for those occurring after birth.

All graphs, data exploration and analyses were carried out in R, version 3.6.3 (R Core Team, 2020). For the modelling with GAM, we relied on the package 'mgcv', version 1.8–31 (Wood, 2011).

5. Estimations, validations and results

5.1. Classification of modern sheep breeds and archaeological populations

The phenotypic characteristics of present-day sheep breeds resulted in the definition of three conformation groups (Table 2; Fig. 4): a group of lightweight and small breeds (Soay, Cameroon and Skudde sheep), a second group of medium-sized and medium-weight breeds (Rasa Aragonesa, Welsh Mountain, Rouge du Roussillon, Karakul and Rhön sheep), and a third group comprising tall, heavy sheep breeds (Leine, German Blackhead and Merino sheep). The two forms of wild sheep, the Asiatic and the European mouflon, exhibit completely different conformations. Both appear light in weight relative to their withers height. Regarding body weight, the Asiatic mouflon falls within the range of the medium-weight conformation group, while the European mouflon overlaps with the light and medium-weight sheep breeds. This is illustrated by the analysis of the trochlear breadth (BT) of the humerus (Fig. 5). Since European mouflons overlap with both light and medium weight conformation groups in domestic sheep, their humeri had to be omitted from further analyses. Another reason for their exclusion is the fact that the individuals curated in the collections experienced quite different living conditions and life histories: most of them come from zoos (mainly those from the SAPM), others from game enclosures and some even from the wild (mainly those from Halle). Furthermore, captive animals often witness inbreeding depressions leading to body mass and size reductions (Laikre, 1999: Table 4). In sum, analyses based on a mixture of free-ranging and confined wild sheep populations must be considered problematic.

Finally, the archaeological populations, for which age predictions will be conducted, need to be classified. According to Fig. 5, the sheep populations of Syene and Aşıklı Höyük match best with the medium-weight category. The prediction model will therefore be based on the data of this conformation group (see Table S1; for the complete dataset classified according to conformation groups see Fig. S1).

5.2. Model estimation and validation

We start the model estimation step by dividing the data up into a training set comprising 70% of the observations and a test set made up of the remaining 30%. Since our main goal is to develop a reliable prediction model, we train our model with the first data set and validate it using the test set. The summary output of the model (Table 3) shows that the model captures the structure of the underlying relationship, with an adjusted R^2 of 0.827 and explained deviance of 84.5% for 17 observations in the training set.

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Table 3

Summary output of the GAM model (edf = estimated degrees of freedom; SE = standard error).

Family: gaussian				
Link function:	identity			
Formula: Weeks_ab_con ~ s(Bd)				
Intercept	Estimate	SE	t value	p-value
	29.1765	0.7562	38.59	6.11E-16
s(Bd)	Approximate	Approximate significance of smooth terms		
	edf	Ref.df	F	p-value
	1.604	1.995	3841	4.16E-08

Таb	le 4	1
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Prediction accuracy of the training dataset.

 ID	(weeks fr	om conception) Prediction	Error
IPE 200b	15	15.48846	0.4884617
IPE 1 2/3	25	29.96097	4.9609716
IPE 21	27	29.80558	2.8055759
IPE 23	35	32.21238	2.7876156
IPE 14	39	40.21476	1.2147629
IPE 25	43	36.25568	6.7443205
HE 2989	44	32.71403	11.2859724

In a second step, we validate our model by predicting the response variable *age* in the test data set and compare the predictions with the real values of the response. In Table 4 we calculated the absolute errors of our prediction comparing with the true values of *age* for the 7 observations in the test data set. The resulting Root Mean Squared Error (RMSE) of the model is 5.5, which is a very small value, indicating the goodness of the prediction. The statistics for the GAM model (Table 3) give a highly significant result for the non-parametric function producing the following regression equation: Age = 29.2 + f(Bd(Dia)). The estimated degrees of freedom (edf = 1.604) are relatively low, illustrating that the shape of the curve is not very complex but still non-linear (Fig. S2). Nonetheless, due to the few observations available, the confidence intervals (CI) are rather wide particularly towards the lower end.

5.3. Age predictions for archaeological populations

The age predictions based on the GAM model provide us with a range between 14 and 39 weeks after conception for the specimens from Aşıklı Höyük and Syene (Fig. 6; Table S2). Since the model is based on relatively few data points, the confidence intervals are rather wide, adding a relatively high amount of uncertainty to the predictions. It can nevertheless be concluded that several of the humeri belonged to foetal animals that died during pregnancy thus provoking abortion. A comparably dense cluster of twelve data points is located around the birth period (week 20-24 after conception) while the data points above the birth period distribute rather evenly (18 instances in week 25-40) (Fig. 6). When considering the chronology, it seems that relative mortality before and after birth was more or less the same in the (early and) middle horizon, while postnatal mortality occurred less frequent in the late horizon (Table 5; Fig. 6). The chi-squared test, however, fails to find an association between lamb mortality and chronology (Chi-squared = 2.3686; p = 0.1238).

The unique case of the lamb foetus from Syene that died during parturition has a predicted age of 23 weeks after conception, which nicely fits the upper range of the birth period (Fig. 6, green data point), thereby strengthening the validity of the model.



Humerus, Bd(Dia) [mm]

Fig. 6. Age predictions for the humeri from Aşıklı Höyük (orange – early and middle horizons; dark green – late horizon; grey – indet. horizon) and Syene (green). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

 Table 5

 Aşıklı Höyük. Frequencies of cases classified by chronology and age-at-death for the chi-squared test statistic.

		Horizon	
		early & middle	late
Cases	prenatal	9	13
	postnatal	10	5

6. Discussion

6.1. A new non-linear model for age predictions

The first aim of this study was to develop a novel approach for age predictions for foetal to infantile lamb bones based on bone measurements, which we exemplified for the distal breadth of the humerus. The range of variation in the modern dataset necessitates the grouping of sheep according to the conformation of the breeds. We therefore developed a work flow to divide modern sheep breeds into three conformation groups and classify archaeological populations according to these groups. While there are enough humerus data available for medium-weight sheep, the dataset is currently too patchy for light and heavy breeds to propose separate models.

We developed a GAM model for the distal breadth measurements of the humerus. The curve described by the model is almost linear as shown by the low edf value. A linear model probably would give rather similar results as suggested by Gillis et al. (2013). However, more data particularly of foetal animals will alter the curve to a more sigmoidal shape so that the GAM approach proposed here will provide more accurate results than a linear model. This is certainly true for other skeletal elements exhibiting later epiphyseal fusion, since in such cases the corresponding section of the complete growth curve will be much larger than in the humerus.

Finally, the successful validation of the model based on the perinatal

lamb from Ptolemaic-Roman Syene confirms the appropriateness of our approach for medium-weight sheep. In the future, the dataset of modern medium-weight specimens of known age needs to be expanded to enhance the model's power and obtain narrower confidence intervals. This is particularly true for the lower end of the curve. Currently only two foetuses with age estimations based on their weight are available. Since their ages are estimated, this adds to the uncertainty of the model in this part. Needless to say, the inclusion of a wide variety of breeds for each conformation group is another major *desideratum* for the future.

6.2. Natural and anthropogenic causes of mortality in foetal and infantile lambs

Three periods in early life of lambs are precarious: late pregnancy, the first week after parturition and weaning. In sheep, infections are responsible for two thirds of foetal losses, i.e., deaths between day 100 after conception and parturition, which therefore pose the biggest risk (Behrens et al., 2001). Infections leading to abortions are caused by a variety of microbial agents, more precisely bacteria (e.g., Brucella spp., Campylobacter spp., Chlamydia abortus, Salmonella spp.), protozoans (mainly coccidia such as Toxoplasma gondii) and viruses (e.g., Bunyaviridae, Flaviviridae), many of which are also known to cause zoonoses (Edmondson and Shipley, 2012). Another third of foetal losses are due to non-infectious causes such as chromosomal re-arrangements, sheep/goat hybridization in mixed herds, stress, nutritional deficiencies and toxic plant ingestions (Edmondson and Shipley, 2012). While abortion rates due to genetic causes are considered negligible, malnutrition as well as stress caused by heat, carnivore attacks and overcrowding in pens have certainly to be considered (Edmondson and Shipley, 2012; Scott, 2015). Quantitative malnutrition in calories and proteins and deficits in certain essential nutrients, such as copper, iodine, magnesium, manganese, vitamin A and selenium/vitamin E can provoke abortions and births of weak lambs (Edmondson and Shipley, 2012).

Turning to the risks after birth, infected lambs and malnourished ewes are generally endangered. Depending on the stage of pregnancy,

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malnutrition in ewes is known to have negative effects on the growth of the foetus (Richardson et al., 1976; Spence et al., 1982). This seems to mainly affect body mass (i.e., weight) and much less the development of the skeleton (McDonald et al., 1977). Since low-weight and small foetuses may also be mistaken for being younger in age than they are, the influence of malnourishment of the ewes on skeletal growth needs to be discussed in future when osteometric data of healthy and malnourished foetuses are available. The radio-opaque lines found in bones of intra-uterine growth retarded foetuses (see Spence et al., 1982) would certainly help to identify corresponding cases in archaeological sheep. Low birth-weight was identified as a significant risk factor for lamb mortality in the first week (Christley et al., 2003; Yapi et al., 1990). Close penning not only induces stress leading to abortions, it also negatively affects the birth process itself and early post-parturition by disturbing the bonding phase between lamb and ewe. This may lead to mismothering, rejection of the lamb or hinder the access of the lamb to the udder causing starvation and finally death of the lambs (Dwyer et al., 2015). With insufficient space, weakly animals are also not able to escape aggressive conspecifics causing additional stressful conditions (Dirksen, 2006). Finally, hypothermia can pose additional threats to outdoor-born lambs and to weak individuals with poor bonds to their ewes in particular (Dwyer et al., 2015).

The third risky phase for lambs in modern production systems occurs during weaning, when lambs and ewes become separated too early and lambs do not get adequate supplemental fodder. Observations of traditional husbandry systems make it extremely unlikely that forced weaning was practiced in (pre-)historic times. Weaning in sheep naturally happens between 100 and 150 days post-partum, which is around 35–42 weeks after conception (Arnold et al., 1979).

Finally, it should not be overlooked that foetal and infantile deaths may also have anthropogenic causes. For instance, the culling of pregnant ewes and/or newborn lambs may have been necessary in times of fodder shortage particularly when the cold season extended into the lambing season (for ethnographic examples see Halstead, 1998).

6.3. Lamb mortality in the early Neolithic sheep population at Aşıklı Höyük

As mentioned above, a significant proportion of bones of foetal to infantile lambs (3.6%) was already noted for early occupation (i.e., upper Level 4) at the site and interpreted as the result of culling pregnant females or of abortions due to inappropriate husbandry conditions (Stiner et al., 2014). Remains of this very young age cohort have been found as well in contexts dating to later site occupation (Levels 3 and 2). Interestingly, in other archaeological cases, human consumption of foetal and neonatal sheep is evidenced by breakage patterns, cut marks and human chewing marks, e.g., in Neolithic and Bronze Age levels in the El Mirador breeding cave in Spain (Martín et al., 2016) and in the Neolithic level in the Pupićina breeding cave in Croatia (Miracle, 2006). Conversely, bones of foetal and infantile animals at AH show neither cut nor chewing marks. Where humeri are broken we are dealing with dry, i. e. post-depositional breaks. Moreover, a surprising amount of humeri are preserved fairly complete. In addition, almost all elements of the skeleton are present including skull, caudal vertebrae and foot bones. Usually, the latter elements are heavily underrepresented in or even absent from consumption refuse. Obviously, sheep that died very young at AH seem to have been discarded in toto. These arguments taken together do not completely rule out human consumption, but certainly build a strong argument against it. Since butchery and dismembering of caprines happened near but outside the settlement in the later phases of site occupation (Peters et al., 2018), the skeletal completeness observed also suggests that the foetal bones did not result from the culling of pregnant females, since in such cases their bodies would have been discarded outside the residential architecture as well. As stated, the presence of extensive layers of compacted dung intra muros confirms that caprines were kept inside the settlement in close confinement over

extended periods of time (Mentzer, 2018). Taken together, our observations allow us to conclude that the foetal and some of the perinatal bones originate from abortions. Such events often happened at night, when the animals are penned in enclosures, which at AH were located within the settlement. The aborted foetuses as well as lambs which died during parturition and in their first weeks were discarded on the middens between the houses. The virtual absence of gnawing marks and the skeletal completeness of these fragile bones also emphasize that neither dogs nor wild carnivores, such as foxes or wolves, had access to the middens inside the settlement (Buitenhuis et al., 2018).

As can be seen from Fig. 6, there is a clear cluster of data points just before and around the lambing date, which suggests that most losses at AH coincided with the first two of the above mentioned precarious periods. As expected, the upper end of predicted ages for the unfused humeri, coinciding with the phase of natural weaning (around 35-42 weeks after conception), does not show a particular cluster (Fig. 6). Lambs surviving late pregnancy and their first week obviously had rather good prognoses. These infantile lambs may have died due to natural causes but also may have been culled for example to remove young males from the flock and thereby reducing disturbances by males during the rutting season. Evidence for sex-specific cullings of young males was found in the ratio of fused and unfused pelves from upper level 4 onwards throughout the occupation of AH (Buitenhuis et al., 2018; Stiner et al., 2014). The colour-coded data points in the graph (Fig. 6; see also Table S2) suggest that lamb mortality was similar in the pre- and postnatal periods during the early and middle occupation horizons while abortions were seemingly more frequent than deaths after birth during the late occupation horizon at AH. This indicates that the livestock keepers were possibly able to improve lamb survival postpartum in the later occupation horizon while problems during late pregnancy and around birth seemingly continued. The non-significant chi-squared test result, however, does not support this impression statistically, which can be due to the rather small number of cases.

From the foetal to infantile humerus assemblage itself it is not possible to draw conclusions on the causes of the premature deaths of lambs. However, another study of the caprine populations at AH found multiple joint diseases affecting the articulations of the limbs (Zimmermann, 2019). These are expressed in form of small lesions on the articular surfaces, e.g., of the humerus, astragalus and calcaneum and peri-articular pathological alterations on the shaft of the femur. Zimmermann (2019) developed a system to determine population profiles of these conditions in order to diachronically trace their course, and identified potential causes which can be compared to those inducing abortions and neonatal lamb mortality. As a result, poor hygiene was found to be one of the root causes for the pathological condition in the femur. Micromorphological analyses of dung deposits at AH provide evidence for dense penning of caprines within the settlement without evidence of regular cleaning (Mentzer, 2018). Caprine stabling on dirty bedding and excrements which are never or rarely mucked out increase the risk of infection by bacteria including Salmonella ssp., Campylobacter ssp., Chlamydia abortus and parasites, such as Toxoplasma gondii (Zimmermann, 2019). Besides microbial infestations, nutritional deficiencies of essential trace elements (particularly copper) and deficits of protein in the fodder additionally facilitate the development of anaemic conditions resulting in intra-articular lesions in the other skeletal elements (humerus, astragalus, calcaneum) (Zimmermann, 2019). Confinement in limited enclosures also causes non-physiological conditions further promoting these micro-lesions (Zimmermann et al., 2018; Zimmermann, 2019).

In our opinion, it is certainly not by coincidence that the same microorganisms and nutritional deficiencies proposed as potential causal factors triggering the arthropathies are known to provoke the abortion and death of neonatal lambs as well. Understandably, dense penning is a significant stress factor instigating aggression and restlessness in flocks, conditions that are known to further worsen intra-articular health and endanger pregnancies and lamb survival as explained above.

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Other stressors already mentioned, i.e. heat and carnivore attacks, as well as chromosomal re-arrangements, sheep/goat hybridizations and poisonous plants as triggering factors are difficult to evaluate and probably did not have a strong impact. Heat, for example, was certainly not an issue during the lambing season (late winter and early spring) on the Central Anatolian plateau with average temperatures of c. -1.5 °C in winter. Carnivore attacks can most likely be ruled out as well, since the flock or at least the breeding animals were obviously penned within the settlement where large carnivores had no access. This was probably even one reason for stalling them near to humans and thereby holding carnivores at bay. Summing up, micro-pathological analysis of caprine bones suggests a range of possible causes for the joint lesions observed, which to a large extent concur with the causes known to provoke late abortions and mortality within the first week of life in lambs. Penning livestock on unremoved excrements seems to be the most likely cause for both situations.

In order to estimate the overall impact of lamb losses on herd survival, however, it would be essential to calculate the rate of lamb losses. In modern sheep production systems, lamb losses amount in average to 15% of total pregnancies, in rare cases such as "abortion storms", i.e., abnormal high incidences of abortions as a result of an epidemic disease, to 40% or more (Dwyer et al., 2015: Fig. 1; García-González, 1979). In archaeological materials it is not possible to assess the rate of lamb losses due to the very nature of these materials, wherein many factors (time depth of the assemblage, overall bone loss, differential survival of elements etc.) cannot be quantified. Presumably, techniques and know-how of breeding and raising sheep successfully likely developed in a long and difficult process of learning by doing (Peters et al., 2014), whereby diagnosing conditions and providing adequate treatment was certainly one of the most challenging tasks. Regarding the intra-articular micro-lesions, herders at AH obviously optimized the management of their flocks considering the significant decrease in lesion frequency and intensity in the sheep populations associated with the late horizon (Zimmermann et al., 2018; Zimmermann, 2019). To what extent the changes brought about, e.g. by pasturing sheep further away from the settlement (Neuberger et al., 2019) or less dense penning outside the residential areas positively affected lamb survival, is difficult to say. The distribution of cases according to age-at-death and chronology (Fig. 6) seemingly indicates that livestock keepers may have successfully reduced postnatal lamb losses towards the end of site occupation at AH although the statistics do not confirm this at present.

Lastly, we return to the special case from Ptolemaic-Roman Syene. The reason for this lamb's death is undisputable given the situation observed in the grave deposit: obstructed in the deformed birth canal of the ewe, the offspring died during an undoubtedly long birth process. In modern sheep medicine, a situation like this is classified as birth trauma due to a difficult or prolonged delivery resulting in hypoxia and consequently stillbirth (Dwyer et al., 2015).

7. Conclusions

Based on a statistically meaningful metric dataset of humeri of modern and archaeological adult sheep and published data on modern breed characteristics, a workflow was developed allowing us in a first step to assign modern sheep breeds to three conformation groups (light-, medium-, heavy-weight) and in a second step to classify archaeological sheep accordingly. Our results show that from an archaeological perspective, medium-weight sheep are particularly relevant for demographic profiling of very young animals. For this group, we constructed a non-linear GAM model using the distal breadth of the humerus that was validated successfully. At present, our database is still somewhat patchy for foetal sheep, and needs to be enlarged in the future. To this extent and for verifying specialists' own specimens, the dataset is made accessible to the archaeozoological community (Table S1).

With the model at hand, we were able to predict ages for the Aşıklı

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Höyük assemblage of measureable humeri (n = 43) and for the Syene lamb. The latter not only confirmed the usability but also the validity of our model. The resulting graph shows two main clusters for the Aşıklı Höyük assemblage identifying the late gestational/perinatal phase and the precarious first week of life as most lethal for sheep managed at the site.

Aetiological considerations relative to the articular micro-lesions observed in early Neolithic sheep identified a spectrum of causal factors for this condition including infections, stress and malnutrition. The dense penning of (breeding?) sheep was found to play a key role in this by causing stressors and amplifying infestations. The agreement of possible factors for these lesions and for foetal and perinatal lamb mortality suggests that these conditions were also responsible for lamb losses. Thereby we catch a glimpse of the problems and difficulties early sheep keepers at Aşıklı Höyük had to face. The analysis showed that towards the later occupation horizon the rate of lesions decreased, implying changes in management of caprine herds. These probably included their pasturing at a distance of the settlement thus increasing locomotion and their general health conditions. It seems that this possibly also improved postnatal lamb survival towards the end of site occupation.

In the future, we intend to enlarge the dataset of modern foetal and infantile sheep in order to fine-tune the model for humeri presented here and to develop ageing models for other skeletal elements for all three conformation groups. Since genetic research is now also targeting pathogens in human and animal skeletal materials and the sediment attached to these, the investigation of pathogens in animal bones will in the future also help to identify the causal infections in foetal and infantile sheep bones from Aşıklı Höyük.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2021.105344.

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