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Pathological and sub-pathological changes in European rabbit bones: Two reference cases to be applied to the analysis of archaeological assemblages

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ABSTRACT

Objective: To provide prevalence data for future comparative analysis of the health status of rabbits (*Oryctolagus cuniculus*) accumulated in the archaeological record.

Materials: Two contrasting assemblages were analysed for pathological and sub-pathological changes: 1) an assemblage of domestic modern rabbit bones; and 2) a non-anthropogenic accumulation of archaeological rabbit remains.

Methods: The lesions observed macroscopically, under magnification, and radiographically in both assemblages are quantified and described.

Results: In the first assemblage, pathological and sub-pathological changes mostly affected the lower limb bones and primarily took two forms: diaphyseal periosteal proliferation and hypervascularised distal physes. Differential diagnosis of the periosteal proliferation suggests that pododermatitis is the most probable cause. In the second assemblage fractures were the most common lesions, but isolated examples of hypervascularised physes, periosteal proliferation, and musculo-skeletal stress markers were also identified. The pathological changes recorded is typical of a naturally-accumulated population of wild rabbits.

Conclusions: The prevalence of pathological and sub-pathological skeletal changes in the rabbits, and thus their health status, are closely related to living conditions. This study demonstrates the value of systematically recording pathologies in rabbit bones.

Significance: We contribute new data to help understand rabbit interactions with humans in the past and also the environment they inhabited.

Limitations: Working with modern samples frequently means only incomplete skeletons are available for study. In these cases lesion prevalence always needs to be interpreted with caution.

Suggestions for further research: Paleopathological studies of rabbit remains are remarkable for their absence. Further exhaustive research in this area is advised.

1. Introduction

The skeletal remains of the European rabbit (*Oryctolagus cuniculus* L. 1758) are abundant on many archaeological sites. This is the case, for instance, on most prehistoric sites from the Iberian Peninsula and the Mediterranean region where rabbits may have played a key role in subsistence, influencing human mobility and demography in the process (e.g. Hockett and Haws, 2002; Stiner et al., 1999; Villaverde et al., 1996). From at least the first century BCE, rabbits were managed and hunted in walled enclosures; there is even evidence that they were deliberately fattened for the table (*De Re Rustica* Book III, xii-xiii, trans. Hooper and Ash, 1979, 489–494). During the medieval period, rabbits were introduced into many parts of northern Europe, where they provided a valuable source of food and fur, and were employed as markers

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of social and religious identity, especially amongst the secular and ecclesiastical elite (Sykes and Curl, 2010, 118–119). The right to keep rabbits in specially constructed warrens was strictly controlled and perhaps best exemplified by the frequency with which medieval poachers were prosecuted for taking them (Bailey, 1988). In theological terms, rabbits had allegorical significance: parallels were drawn between their underground habit, fecundity, and emergence from burrows, and Christian notions surrounding concerning salvation and resurrection (Stocker and Stocker, 1996). Thus, as Stocker and Stocker (1996: 270) describe, "in its warren, like human corpses in a catacomb, the rabbit is the corporeal awaiting eternal life". Notwithstanding their symbolism, rabbit farming remained an important component of the rural economy in many parts of Europe into the early twentieth century (Williamson, 2006:6−13).

Despite their abundance on archaeological sites, in-depth studies of archaeological rabbits have only been pursued in the last few decades (e. g. Callou, 2003; Cochard, 2004; Hockett and Haws, 2002) and there have been no analyses of diseases and injuries in past rabbit populations. Yet, the recognition of the health status of rabbits accumulated in the archaeological record may provide key data regarding their relationship with humans in the past. To take just three examples: the prevalence of healed fractures might reveal trapping strategies; high stocking densities within warrens could increase infectious disease transmission; and managed warrens stocked from a small nucleus, and possibly over-hunted wild populations, may be more predisposed to developmental anomalies. While not all diseases are reflected in the skeleton, the study of pathologies in animal bone assemblages provides a window through which some of these issues could be explored.

Successful paleopathological analysis partly rests on the identification of changing temporal and/or spatial patterns of lesion prevalence. For this reason, it is imperative that the frequency and character of pathologies in known-history populations is determined, so that changes related to sex, age, population genetics, environment, disease, and human management can be teased out (Thomas and Mainland, 2005). Studies of the nature and prevalence of lesions in modern comparative populations of animals forms an essential component of this research, particularly in separating what is 'pathological' from what is 'non--pathological' (e.g. Bartosiewicz et al., 1997; Bendrey, 2007; Darton and Rodet-Belarbi, 2018; Fabiš and Thomas 2011; Levine et al., 2000; Niinimäki and Salmi, 2016; Rafuse et al., 2013; Siegel, 1976; Taylor and Tuvshinjargal, 2018; Thomas and Grimm, 2011; Zimmermann et al., 2018). However, modern comparative collections do not exist for many species and some lesions are not observed in modern animal populations. This partly reflects the fact that, today, most diseases are treated or the animal is slaughtered before skeletal tissues become involved. Moreover, many types of skeletal lesions do not affect the health status or productivity of animals, and therefore lie outside the purview of veterinary pathologists. In such cases, it is necessary to rely upon the methodical analysis of large samples of animal bones from archaeological sites (e.g. Holmes et al., 2021; Thomas and Johannsen, 2011), to better understand the variability of lesion expression and the factors influencing their development.

In recognition of these facts, we present the analysis of pathological and sub-pathological changes in two samples: (1) an assemblage of modern rabbit bones recovered from an experimental taphonomic study; and (2) a non-anthropogenic archaeological accumulation of rabbit bones. In doing so we seek to: obtain new information about the diseases affecting the skeleton of this taxon; and provide prevalence data of different kinds of rabbit assemblages to be used in the comparative analysis of archaeological rabbit remains.

2. Materials and methods

The first sample comprises modern rabbit bones recovered from an experimental study to assess the taphonomic signature of red foxes (*Vulpes vulpes*; Lloveras et al., 2012). Four foxes kept in captivity at the wildlife recovery center of Torreferrussa in Barcelona (Spain) were fed with complete rabbit carcasses. These animals were adult and sub-adult domestic specimens recovered from a nearby rabbit farm. The rabbits were very large and had been bred to provide meat; however, the animals in this sample were those that had died for different reasons, normally related to poor living conditions. Material used here comes from the remains that were not ingested by the foxes. Most of the recovered remains were limb bones and, in some cases, they were still attached to the skin of the rabbit. Material was rehydrated, boiled to facilitate removal of any remaining soft tissue carcasses, and left to macerate in the enzyme Neutrase. After a few hours, they were cleaned under running water and air-dried.

The second sample is a hand-collected archaeological assemblage of rabbit remains from Dudley Castle, West Midlands (UK) (Fig. 1). These remains were recovered from a group of associated contexts within the fill of a garderobe (toilet) shaft, built into the east (outer) wall of the domestic range of the castle. The garderobe appears to have been constructed in the 14th century to service the Great Chamber on the first floor, with the waste flowing out into the moat (Linnane, 2021.:99). The lower fills of the garderobe were organic while the upper fills appeared more like destruction rubble; all the finds indicate a 16th-century date (Linnane, 2021.:100). The animal bones from this site were originally published by Thomas (2005), although only a restricted suite of skeletal elements was recorded (following Davis, 1992), hence the considerably larger sample size in this study. The density of rabbit bones in these contexts, combined with an even representation of body parts and the lack of butchery marks, supported the interpretation that the accumulation built-up following abandonment and in-filling of the shaft, which

Fig. 1. Map showing the location of Dudley Castle.

would have made a suitable artificial warren (Thomas, 2005:66). This theory of abandonment was supported by the presence of dense accumulation of the bones of jackdaws, a gregarious species who were presumably nesting in the abandoned upper parts of the garderobe (Thomas, 2005:73).

In both samples, bones were anatomically determined (to element and side) and the number of skeletal elements (N) was calculated. Three states of epiphyseal fusion were captured to assist in the determination of age at death: unfused; fusing; and fused. Ontogenic age was established using the rabbit fusion data synthesised by Jones (2006) with supplementary data for lumbar vertebrae extrapolated from the data provided by Taylor (1959; Table 1) for the sixth and seventh lumbar vertebrae. Pathologies were recorded following a modified version of the recommendations of Vann (2008) and Vann and Thomas (2006). This approach advocates fine-grained, systematic macro-morphological examination of bones for pathologies. The precise anatomical location of each lesion was described, with explicit reference to the presence/absence of bone formation and/or destruction, the texture of the surface, and the granularity of the margins. An assessment of the degree of remodeling at the time of death was made and qualitative description was supplemented with quantitative information concerning the size of each lesion. Sub-pathological features, including articular depressions (see Thomas and Johannsen, 2011), and changes with less certain status (e.g., hypervascularised physes), were also recorded since they were observed during analysis and their connection with pathologies *sensu stricto*, merited investigation. Gross and light microscope (10x-40x magnification) morphological analysis was supplemented with radiographic examination where appropriate. The radiographs were taken with Philips Diagnost® medical radiological equipment, at 50 kilovolts (kV) and 5 mA/second (mAs) settings, with a focus-plate distance of 100 cm. Digital radiological AGFA MultiSync LCD 18805X® equipment was used for processing, adjusting the brightness and contrast of the image until the maximum quality was achieved. Bone measurements were taken using the standards set forth by von den Driesch (1976).

For the archaeological assemblage from Dudley Castle four taphonomic variables were also recorded: the presence/absence of butchery, burning and carnivore gnawing, and the preservation condition of the bones. The first three were recorded according the methods described in Lloveras at al. (2009, 2021). The latter was recorded following the four-point scale developed by Harland et al. (2003):

1) Excellent: majority of the surface fresh or even slightly glossy; very localized powdery patches;
2) Good: bone surface lacks fresh appearance but solid; very localized flaky or powdery patches;
3) Fair: surface solid in places, but flaky or powdery on up to 49 % of the specimen;
4) Poor: surface flaky or powdery over 50 % of the specimen.

The minimum number of individuals (MNI) was determined by considering element, side, anatomical zone (following the eight-zone protocol developed by Serjeantson (1996)), and state of epiphyseal fusion.

The statistical significance of differences in pathological and sub-pathological changes was tested using the chi-squared test. Metrical data were tested using the non-parametric Mann-Whitney *U* test, in recognition of the fact that not all of the variables were normally distributed (Sokal and Rohlf, 1980). All statistical analyses were conducted using SPSS Statistics.

Table 1
Timing of epiphyseal fusion in selected rabbit bones (after Jones, 2006; Taylor, 1959).

Epiphyseal fusion	Bones
ca. 3 months	Distal humerus, proximal radius
ca. 5 months	Proximal ulna, distal femur, distal tibia
9–10 months	Proximal humerus, distal radius, proximal femur, proximal tibia, distal ulna
15–33 months	Lumbar vertebrae

3. Results

3.1. *Sample 1 – modern rabbit bones*

A total of 639 bones and teeth were recovered, from a minimum of 11 animals. Only limb bones (including two complete shaft and distal parts of the long bones in addition to metapodia and basipodia elements), caudal vertebrae, and a few mandibles were present (Table 2). The ageing data indicates that all animals died after the first 5 months of life. The presence of 20 % of unfused distal radii and distal ulna indicate that these animals were younger than 10 months. The rest of bones derived from animals older than 10 months; however, the lack of lumbar vertebrae in the sample prevents us from knowing if there were any individual over 33 month of age or not (Table 1, Taylor, 1959).

The number of bones displaying pathological or sub-pathological changes was 136: 21 % of the recovered sample (Table 2). Changes were mostly observed in the distal parts of the long bones, carpal/tarsal bones, and the proximal part of metapodials. The most affected bone was the calcaneum, all of which exhibited lesions (Fig. 2). Phalanges were the most abundant elements in the sample, but only 3.3 % of the proximal and distal phalanges exhibited pathological or sub-pathological changes.

3.1.1. *Pathological and sub-pathological changes*

Pathological and sub-pathological changes were partitioned into two groups: those that exhibited bone destruction, and those that exhibited

Table 2
Numbers (N), minimal number of elements (MNE), and number (N Path) and percentage (%Path) of pathological and sub-pathological elements recorded in both samples.

	Sample 1				Sample 2			
	N	MNE	N Path	% Path	N	MNE	Path	% Path
mandible	2	2	0	0.0	32	30	0	0.0
cranium	0	–	–	–	59	13	0	0.0
lower molar	8	8	0	0.0	0	–	–	–
atlas	0	–	–	–	4	4	0	0.0
axis	0	–	–	–	2	2	0	0.0
cervical vertebra	0	–	–	–	15	15	0	0.0
scapula	0	–	–	–	35	35	1	2.9
humerus	1	1	0	0.0	47	42	0	0.0
radius	7	6	5	83.3	26	26	3	11.5
ulna	8	6	5	83.3	31	31	1	3.2
carpal bone	43	43	9	20.9	0	–	–	–
metacarpus	24	24	3	2.4	5	5	0	0.0
thoracic vertebra	0	–	–	–	77	77	0	0.0
ribs	0	–	–	–	128	128	2	1.6
lumbar vertebra	0	–	–	–	93	93	0	0.0
sacrum	0	–	–	–	11	11	1	9.1
pelvis	0	–	–	–	41	39	2	5.1
femur	0	–	–		39	32	0	0.0
tibia	21	16	12	75.0	43	40	3	7.5
calcaneum	18	16	16	100.0	9	9	0	0.0
astragalus	19	17	12	70.6	0	–	–	–
other tarsal	59	58	45	77.6	0	–	–	–
metatarsus	80	79	22	27.8	76	76	0	0.0
phalanx 1/2	216	211	7	3.3	4	0	0	
phalanx 3	104	104	0	0.0	0	–	–	–
caudal vertebra	29	29	0	0.0	0	–	–	–
TOTAL	639		136	21.3	777		13	

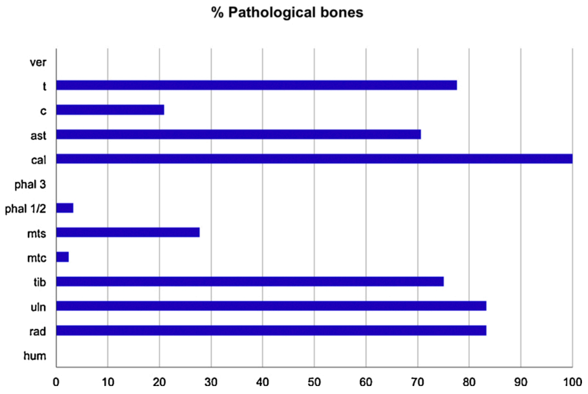

Fig. 2. Percentage of pathological and sub-pathological rabbit remains in Sample 1. This sample included a total of 639 bones. The absolute number of each skeletal element is provided in Table 2. Abbreviations; hum: humerus, rad: radius, uln: ulna, fem: femur, tib: tibia, mtc: metacarpals, mts: metatarsals, phal 1/2: phalanges 1/2, phal 3: phalanges 3, cal: calcaneum, ast: astragalus, c: carpal bone, t: tarsal bone, ver: vertebrae.

bone formation. A total of 132 specimens exhibited bone destruction: one with articular depressions and 131 with 'porosities' (after Vann and Thomas, 2006). A total of 63 bones displayed bone formation: five enthesophytes, eight bone ridges, and 50 with periosteal proliferation. On the whole, the most abundant lesions were 'porosities' and periosteal proliferation which were recorded on 67 % and 25 % of affected bones respectively (Fig. 3). Three articular depressions of type 1, following Baker and Brothwell (1980:109–114), were found on the medial, lateral, and centre of the distal articulation of one tibia (Table 3, Fig. 4A). This type of lesion could be a manifestation of articular osteochondrosis or an anatomical variant with no pathological significance (Thomas and Johannsen, 2011).

Five cases of enthesopathy and eight bone ridges were recorded (Table 3, Fig. 4B–C). Enthesopathies describe new bone formation at the attachment sites of ligaments and tendons. These ossifications occur in response to excessive or repeated ligament or tendon strain, or with advancing age to stabilise the connective tissues. The bone ridges probably also represent ossifications along the length of connective tissues or membranes. Together, these lesions were present on 2% of the recovered sample and on 9.6 % of affected elements. The skeletal elements most affected by these lesions were the calcaneum, distal epiphysis of the ulna, radius, and tibia. Bone ridges were visible on the radiographic analysis as a narrow sclerotic line (Fig. 4G–H).

Periosteal proliferation was present as a plaque of new bone (both woven and lamellar bone were recorded) extending across non-articular surfaces (Fig. 5A–E). Periosteal proliferation forms when the osteogenic properties of the periosteum are activated by direct or indirect infection or inflammation. This lesion was recorded on 50 cases affecting 7.8 % of the whole sample and 36.8 % of the pathological and sub-pathological elements. Tarsal bones and particularly calcanea followed by astragali were the most affected elements (Table 3). Calcanea were the most affected bone presenting in many cases large areas of profuse new bone formation occupying the entire plantar surface. The periosteal proliferation was clearly visible on radiographs as a diffuse slightly opaque layer extending beyond the cortex.

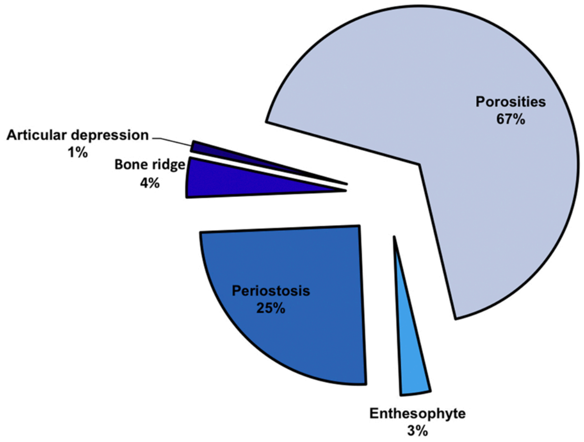

Fig. 3. Percentage of different types of pathological and sub-pathological changes recorded in Sample 1 ($n = 136$).

Table 3
Numbers of skeletal elements affected by the different type of pathological and sub-pathological changes in Sample 1. AD: articular depression, PO: porosities, EN: enthesophytes, BR: bone ridge, PE: periosteal proliferation.

SAMPLE 1	AD	PO	EN	BR	PE
radius	–	4	1	1	2
ulna	–	5	–	1	2
tibia	1	12	2	2	2
metacarpus	–	3	–	–	0
metatarsus	–	24	–	–	2
phal 1/2	–	7	–	–	0
calcaneum	–	14	2	4	15
astragalus	–	12	–	–	9
carpal bone	–	8	–	–	1
tarsal bone	–	42	–	–	17
TOTAL	1	131	5	8	50

The 'porosities' observed consisted exclusively of multiple small nutrient foramina. A total of 131 cases were recorded (Table 3, Fig. 4D–F), almost 21 % of the whole sample and 96 % of the sample exhibiting pathological and sub-pathological changes. They were mainly situated on the distal part of long bones, especially around the epiphysis: the articular surface was unaffected. The radius, ulna, and tibia were affected equally. More than 60 % of calcanea, astragali, and small tarsals also displayed multiple foramina across all surfaces with the exception of the articular surface. They were also present in metapodials, especially on the proximal part; metatarsals (30 %) were more affected than metacarpals (12.5 %). Finally, some carpals (19 %) and a few phalanges (3%) also exhibited multiple small foramina. These changes were radiographically visible (Fig. 4I–J), appearing as a circle of sclerotic bone surrounding a radiolucent area indicating that they penetrate through the bone. In some cases, the macroscopically recorded foramina were not visible on the radiograph, particularly on metapodials.

On the whole, hind-limb bones were more affected by lesions than forelimb bones. These differences were observed in both 'porosities' and other alterations (Fig. 6). This is particularly evident when comparing carpal bones and metacarpals against tarsal bones and metatarsals. The results of a chi-squared test applied to compare the different proportions registered showed that differences are highly significant (% of 'porosities': $\chi^2 = 18.46$; $P < 0.001$; and % of other alterations: $\chi^2 = 8.64$; $P < 0.003$).

Another feature of this sample is that right bones were clearly more affected than the left (64 % compared with 36 %, see Table 4). This difference is highly statistically significant ($\chi^2 = 24.73$; $P < 0.001$). Not all pathological or sub-pathological changes exhibited asymmetric presentation, however (Table 5): it was only periosteal new bone formation (70 % right) and 'porosities' (66 % right). Co-occurrence of these changes in the same specimens suggests they are associated.

To test possible morphometric differences between left and right-side elements a basic biometric analysis was conducted (Fig. 7). It revealed that the average left sided measurements were larger than the right, and that this was more significant for the width measurements (tibia SD), than it was for the length measurements. This was supported by statistical testing; a Mann-Whitney *U* test revealed a significant difference in SD measurements ($U = 1$; $P = 0.0217$) even despite the very small sample size; no statistical difference was present in length measurements ($U=7$; $P=0.2948$).

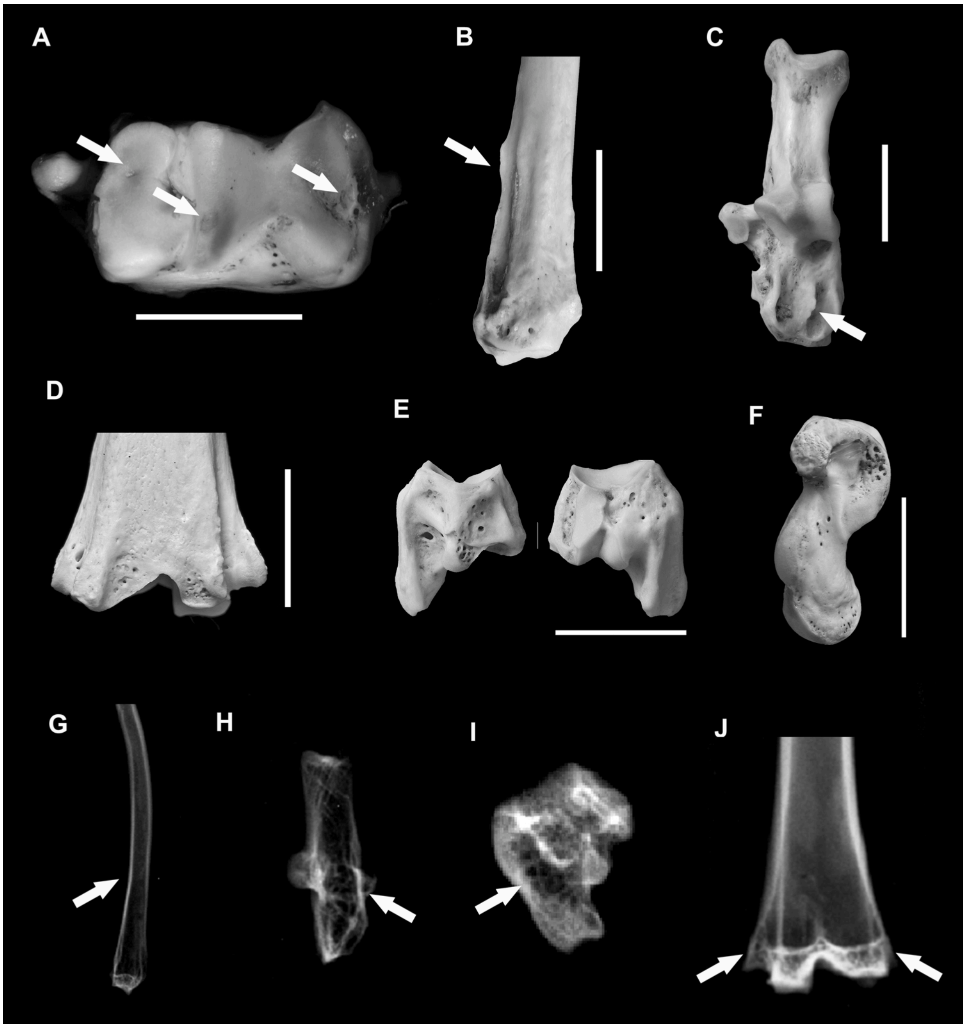

Fig. 4. Examples of bones exhibiting pathological and sub-pathological changes from sample 1. A: articular depressions in a distal view tibia. B: bone ridge affecting the distal part of a radius (caudal view). C: dorsal view of a calcaneum with an enthesophyte. D, E, F: tibia (caudal view), navicular (lateral and medial views) and astragalus (medial view) affected by porosities. Enthesopathies (G: radius medial view, H: calcaneum lateral view) and porosities (I: navicular lateral view, J: tibia cranial view) observed on RX plates. Scale bar = 1 cm.

3.1.2. Interpretation

As noted above, enthesopathies usually develop in response to biomechanical strain at ligament/tendon attachment sites. It is curious to find these lesions in the rabbits studied here since they were kept in captivity. Nevertheless, such lesions may simply reflect the effects of repetitive strain on soft tissue and bony structures. It has been demonstrated, for example, that the scratch reflex, or thumping, movement of the rabbit hind limb resulted in histological changes consistent with localized Achilles tendon inflammation (Barr and Barbe, 2002). In this study, most enthesopathies were registered in the calcaneum and, thus, they may relate to this reflex movement.

Periosteal proliferation is localized in the bones of the feet, especially in the hindlimb. A survey of clinical literature shows that the most likely disease is pododermatitis; in rabbits this usually affects the bottom of the hind feet and hocks (the lower part of the back leg that touches the ground when the animal is sitting). Pododermatitis or 'sore hocks' describes the inflammation and/or infection of the skin and connective tissue of the foot. The condition usually presents as a unilateral or bilateral, chronic, granulomatous, ulcerative dermatitis of the plantar metatarsal surface. The lesion begins as an area of alopecia and erythema, and then progresses to erosions, and ulcerations. The ulcers often become secondarily infected, and the bacterial infection has the potential to spread to underlying bone, resulting in osteomyelitits and sepsis (Drescher and Schlender-Bobbis, 1996; Harcourt-Brown, 2001; Hoppmann and Barron, 2007). The disorder can be idiopathic, although a number of medical conditions are known to cause animals to develop pododermatitis: allergic dermatitis; autoimmune skin disease; trauma with a secondary infection (bacterial and/or fungal); and neoplasia. The most common causes in rabbits are lack of movement, abrasions followed by infection, inadequate diet, and poor sanitation (Harcourt-Brown, 2001; Hoppmann and Barron, 2007; De Jong et al., 2008). The problem is more common in large, mature animals (Percy and Barthold, 2007, 299).

As far as periarticular 'porosities' are concerned, they strongly indicate hyper-vascularity of the physis. Porosities are clearly long-standing since they present themselves as a circle of sclerotic bone surrounding a radiolucent area indicating that they penetrate through the bone. The co-occurrence of foramina and periosteal new bone formation, and the similarity in the asymmetry of their presentation (Table 5) suggests they are associated. We postulate that the hyper-vascularity developed in response to the need for additional blood flow as part of the immune response to the chronic inflammation of the periosteum of affected elements.

The differences in tibia measurements attest to directional asymmetry: where one side of a pair of morphological structures is consistently larger than the other. Directional asymmetry has been observed in the skeletal elements of many species, with the right forelimb often being dominant (Jolicoeur, 1963; Singh, 1971; Leamy, 1984, 1999; Alvarez, 1995; Auerbach and Ruff, 2006). However, it is worth noting that crossed symmetry of the contralateral limb is commonly observed in rabbits and other species (Singh, 1971; Auerbach and Ruff, 2006). Unfortunately, the composition of our sample meant it was not possible to establish if the left-sided dominance extended to other elements or if the examined individuals exhibited contralateral asymmetry. The fact

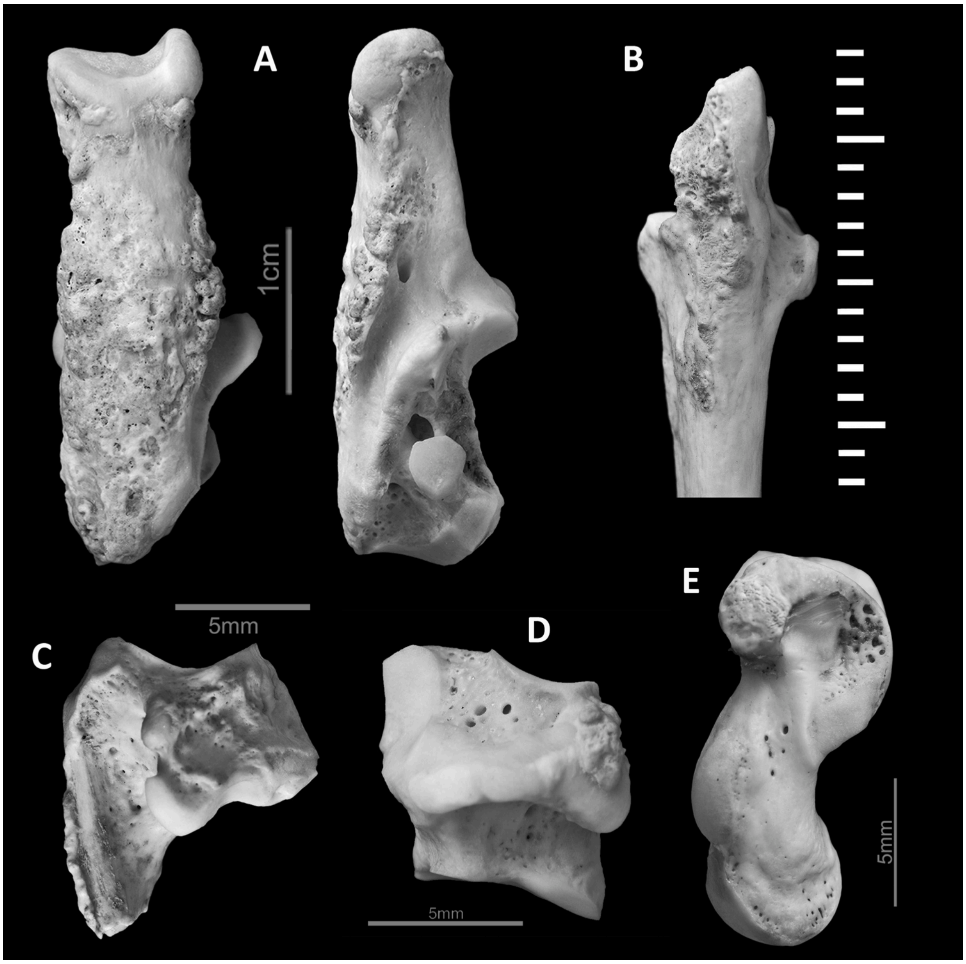

Fig. 5. Different rabbit bones from Sample 1 affected by periosteal proliferation. A: calcaneum ventral and dorsal views, B: metatarsal medial view, C: navicular medial view, D: cuboid dorsal view, E: astragalus medial view.

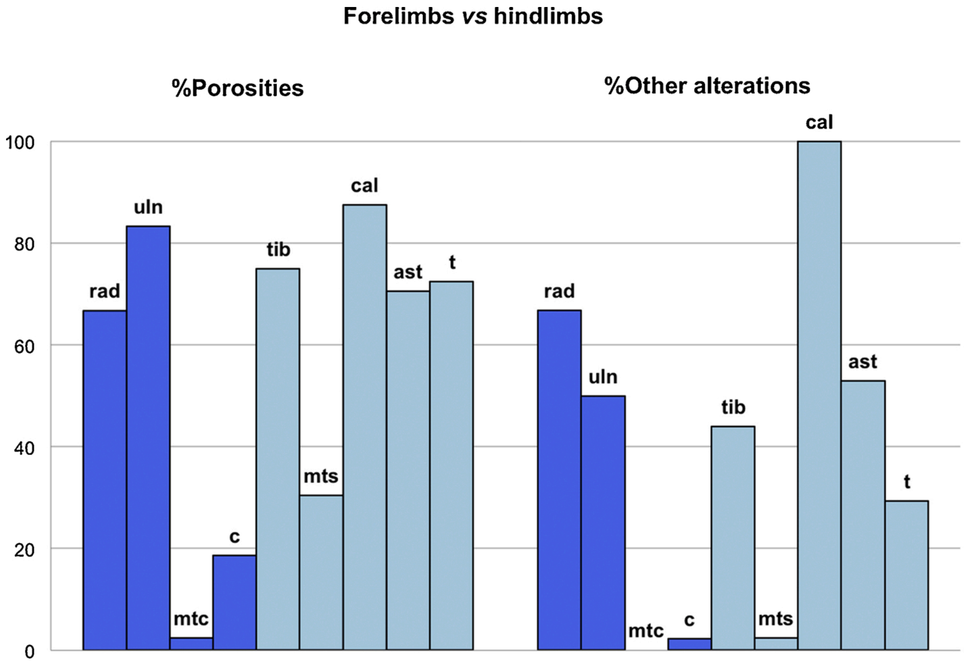

Fig. 6. Percentage of fore limb versus hind limb elements showing 'porosities' and other alterations in Sample 1. The MNE for limb bones was 265, 79 forelimb and 186 hindlimb elements. For abbreviations see caption of Fig. 2.

Table 4
Numbers of sided skeletal elements affected by at least one pathological or sub-pathological change in Sample 1.

SAMPLE 1	Total	Left	Right
radius	5	3	2
ulna	5	3	2
tibia	12	5	7
metacarpus	3	0	3
metatarsus	22	4	18
phal 1/2	7	0	7
calcaneum	16	8	8
astragalus	12	5	7
carpal bone	9	2	7
tarsal bone	45	19	26
TOTAL	136	49	87
%		36 %	64 %

Table 5
Numbers of pathological and sub-pathological cases by side in Sample 1.

SAMPLE 1	Left	Right
Articular depression	1	0
Porosities	45	86
Enthesophytes	3	2
Bone ridge	4	4
Periosteal proliferation	15	35
TOTAL	68	127
%	35 %	65 %

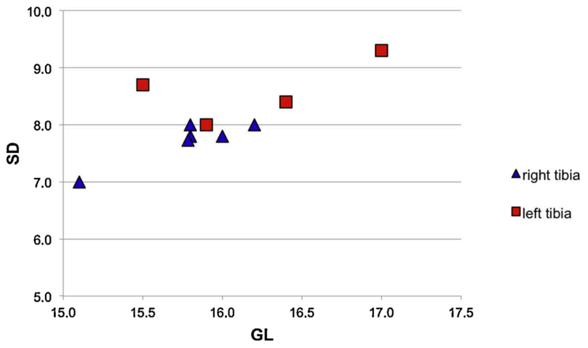

Fig. 7. Biometric analysis of left- and right-sided tibia measurements (after von den Driesch, 1976). Scale in mm.

that the directional asymmetry in the presentation of pathological and sub-pathological changes (Table 4, Table 5) is the reverse of the pattern observed in the metrical data, would suggest these phenomena are unrelated.

Directional asymmetry in skeletal elements can be inherited (Palmer and Strobeck, 1992; Palmer, 1994), occur as a consequence of remodelling in response to unequal mechanical loading (e.g. Auerbach and Ruff, 2006), or have an "an overwhelmingly environmental origin" and thus provide a potential indicator of developmental stability (e.g. Leamy, 1999, 154). Irrespective of the cause, excessive asymmetry of elements with a locomotor function is "selectively disadvantageous" (Leamy, 1984, 588); thus, it is likely that such characters (whether acquired or inherited) are only likely to persist in captive-bred populations.

3.2. Sample 2 – archaeological sample

A total of 777 rabbit bones were recovered from the garderobe at Dudley Castle, representing a minimum of 25 animals (Table 2). The absence of butchery and burning marks, strongly supported the original suggestion (Thomas, 2005, 66), that this is a non-anthropogenic, primary accumulation of rabbit bones. This is further supported by the absence of tooth/beak marks and digestion damage, indicating that carnivores, owls, and raptors were not responsible for the accumulation (Lloveras, 2021). The preservation of the bones was mixed, some specimens exhibited a fresh, glossy appearance, while others were very poorly preserved with extensive cortical destruction; the majority, however, only showed localized abrasion (Fig. 8).

The distribution of anatomical elements is skewed by the fact that the bones were collected by hand: thus, carpal and tarsal bones, and phalanges are poorly represented, and metatarsals were much more abundant than metacarpals (Fig. 9). Sieving experiments have demonstrated that the recovery of metacarpals requires a mesh smaller than 6 mm (Bourdillon, 1998:143). Nevertheless, all parts of the body are present, revealing that the deposit comprises the remains of complete animals. The ageing data for rabbits (Fig. 10) indicates that the majority of animals died within the first 33 months of life; however, 20 % of lumbar vertebrae exhibited fused anterior and posterior plates, indicating the presence of some animals exceeding 33 months of age (Taylor, 1959). In addition to the presence of 20 % unfused proximal radii and distal humerii deriving from animals less than three months old, six bones were very small and appear to represent perinatal mortalities: it is likely that the remains of such young animals are under-represented given the recovery bias against small bones (Fig. 9). While medieval monks favored the consumption of newly born or unborn rabbits, since the aqueous uterine environment resulted in their classification as 'fish' and thus consumable on fast days (Salisbury, 1994:52), the age data are consistent with natural fatalities within a breeding population. In an experimental study of an English warren over a five-year period, Lockley (1961) noted that the oldest buck lived to be four years old, while the oldest doe lived to three years and eight months. Excluding the original breeding population, the average life expectancy was one and a half years, with anywhere between 29 % and 65 % of rabbits surviving their first eight months (Lockley, 1961:415, 417).

3.2.1. Pathological and sub-pathological changes

Only thirteen pathological or sub-pathological bones were identified, representing 1.7 % of the entire assemblage. Six changes were recorded: fracture; joint disease; periosteal proliferation; periarticular porosities; enthesopathies; and bone ridges. The numbers of unaffected bones with the same anatomical zone(s) are given in parentheses following the description of each lesion to provide a precise indicator of prevalence, because not all bones were complete.

Six bones exhibited trauma: a pelvis; the distal diaphysis of a paired radius and ulna; a tibia; and two ribs. The left pelvis (n = 30; Fig. 11A) sustained a multiple fracture: a complete, transverse fracture through the cranial (acetabular) branch of the pubis; and a complete transverse fracture through the caudal branch of the pubis. The trauma caused the

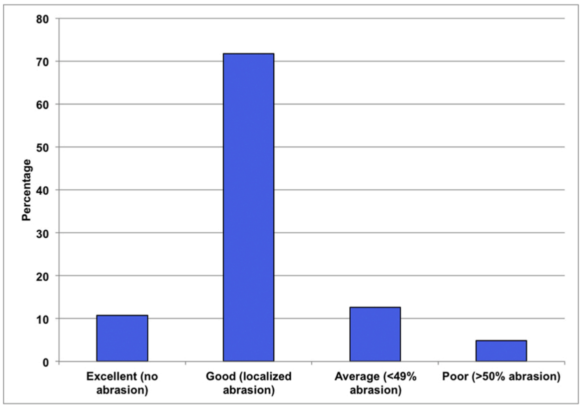

Fig. 8. Preservation of the rabbit bones from Dudley Castle (after Harland et al., 2003).

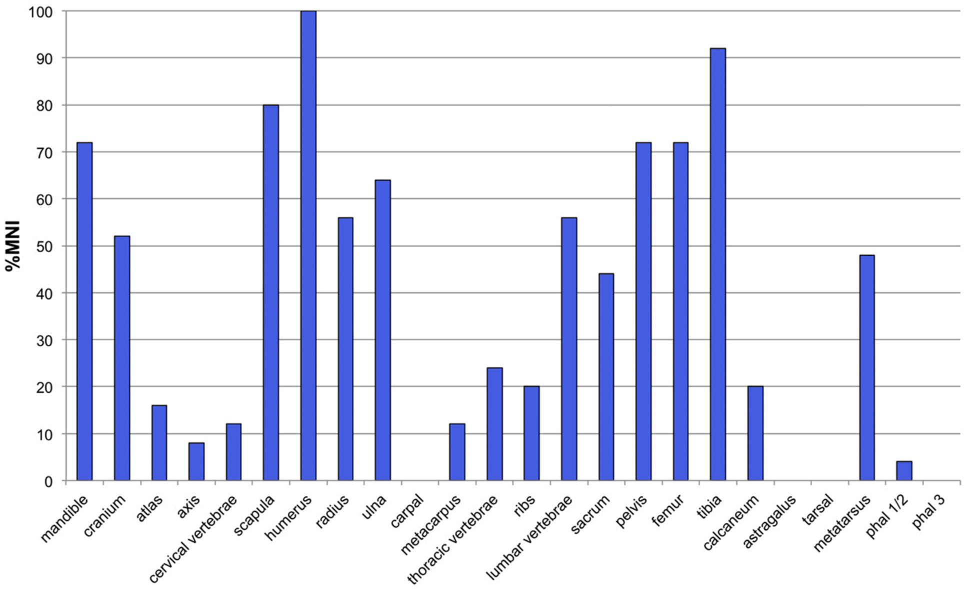

Fig. 9. Representation of body parts in the rabbit bone assemblage from Dudley Castle expressed as %MNI.

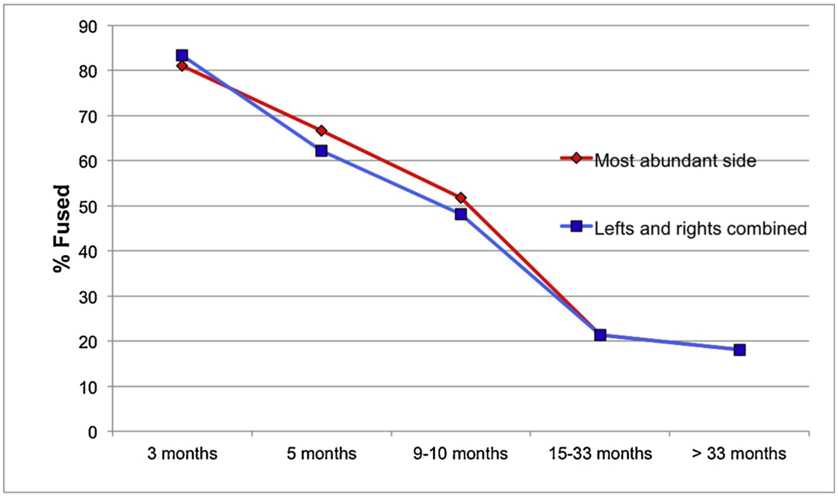

Fig. 10. Percentage of fused rabbit bones in the age categories following Jones (2006, Table 1) and Taylor (1959).

caudal displacement of the pubis and the permanent separation of the caudal branch of the pubis, as evidenced by necrosis at both fractured ends. The latter must have significantly disrupted the pubic symphyseal joint. Callus has formed around the fracture on the cranial branch of the pubis, but the line of fracture is still visible and the new bone is woven and disorganized, indicating that healing was on-going at the time of death. New bone formation (periosteal proliferation) also occurred around the ischial tuberosity and along the lateral and dorsal aspects of the cranial branch of the ischium, which suggests secondary inflammation of the periosteum. There are no secondary degenerative changes to the acetabulum; this could suggest that the afflicted limb was not used following the fracture, or that the animal died before osseous changes in the joint could occur. The former seems more likely, given the fact that that the contralateral pelvis and articulating sacrum (both recovered from the same context) showed evidence of adaptive remodelling. The right pelvis (n = 30; Fig. 11B) exhibited new bone formation around the margins of the auricular surface, numerous lytic cavities (1–3 mm in diameter), and eburnation; these changes are mirrored in the articulating auricular surface of the sacrum (n = 6).

A complete transverse fracture was observed through the distal metaphysis of a paired right radius (n = 25) and ulna (n = 22; Fig. 11C) from an animal less than 9–10 months old. The fracture line is visible in both specimens and they both exhibited profuse, woven callus formation, indicating that the lesion was active at the time of death. At least three draining sinuses (cloaca) were present within the callus of the radius and one in the ulna, suggesting that this was an open (compound) fracture that resulted in secondary infection. The fractured bones were not displaced and no foreshortening occurred, presumably because the adjacent bones acted as natural splints. The elbow and radio-ulnar joint was unaffected by secondary degenerative joint disease; however, a ridge of new bone formation on the cranial surface of the ulna, indicates ossification at the attachment site of the interosseous ligament (which firmly unites the radius and ulna), perhaps in response to inflammatory stimulation of the periosteum, and/or to compensate for altered loading consequent to the fracture.

Other fractures recorded include a tibia with a mid-shaft greenstick fracture (n = 32; Fig. 11D), that had caused the bone to bend in a cranial direction. A 5 mm ridge of new bone projects along the tibial crest of this specimen, and appears to represent the ossification of a ligament or tendon attachment, presumably for biomechanical compensation

Fig. 11. A: Multiple fractures through the caudal and cranial branch of the left pelvis. B: Auricular surface of the contralateral pelvis shown in A, exhibiting osteophytosis, eburnation, and destruction of the articular surface. C: Transverse fractures of a paired radius and ulna; the longitudinal ridge of bone on the ulna is caused by the ossification of the attachment of the interosseous membrane. D: Greenstick mid-shaft fracture of a tibia, with a 5 mm ridge of new bone projecting along the tibial crest. Scale bar = 1 cm.

following the changed angulation of the bone. Two ribs (n = 128) presented complete transverse fractures through the costa. Callus had begun to form, but the broken half of ribs was missing, suggesting that the lesions were active at the time of death.

Periosteal proliferation was observed extending approximately 10 mm along the superior border (margo superior) of a scapula (n = 15), between the neck and the ascension of the spine. It is possible that the new bone formed in response to focal soft tissue trauma. One distal radius (n = 25) and one distal tibia (n = 15) exhibited multiple distal periarticular' porosities', while another fused radius and tibia exhibited new bone formation. The radius (n = 25) has a longitudinal ridge of bone running along the caudal surface and provides a further example of the ossification of the attachment of the interosseous connective membrane. The distal epiphysis also exhibited multiple vascular channels, indicating increased blood flow. The tibia (n = 15) has a smooth, discrete enthesophyte on the lateral malleolus, which most likely developed in response to increased laxity or strain of the tendons of the peroneal muscle which run through the notch on the caudal side of the malleolus (Bensley, 1910:107).

3.2.2. Interpretation

Trauma was directly responsible for 46 % of the pathological/sub-pathological sample from Dudley Castle and implicated in the osseous changes observed in three further specimens (a pelvis, sacrum, and scapula). Four types of traumatic injury can be identified (after Baker and Brothwell, 1980:82): human-induced; inter- and intra-species interaction; accidental; and pathological.

With respect to the Dudley Castle sample, it is possible to rule out pathological fractures because none of the specimens exhibited lesions indicative of diseases that result in reduced mineral density, such as neoplasia and osteoporosis. Disentangling the other causes is challenging, since acute trauma arising from different injurious events can present identically. Clinical studies are helpful, in as much they reveal some of the potential causes of fractures in rabbits, with the caveat that they pertain to captive animals. Such studies have revealed that rabbits are susceptible to hind-leg and thoracolumbar fractures, which can occur as a result of: improper handling; the animal kicking out whilst struggling; and hind-limb thumping, especially in calcium-deficient animals (Richardson, 2000:85). Heard (2007:647) further adds that distal tibia fractures are often caused when a rabbit falls and that leg fractures occur when an animal gets its hind-limb trapped. Given this information, it is entirely feasible (although admittedly speculative) that the greenstick fracture in the tibia was a consequence of thumping activity in a young, and therefore inadequately mineralized, individual. With regards to the fracture in the paired radius and ulna this may have occurred when the animal got its legs caught, either accidentally or as a result of attempted trapping/ensnaring. While the assemblage appears to have accumulated naturally, it is conceivable that some injuries were directly or indirectly the result of human action: for example, as a consequence of a failed attempt to capture the animals; or due to predation by cats and dogs living in and around the site. The cause of the fractured pubis remains obscure. The fact that the fracture line is still visible in five out of six bones with traumatic injury, indicates that the animals died while healing was underway; perhaps as a consequence of the secondary infection visible in the case of the radius and ulna, or the limits placed on mobility in the case of the pelvis.

The occasional nature of the other lesion types in the Dudley Castle sample and their multi-factorial etiology, makes it impossible to determine anything more specifically regarding their pathogenesis.

4. Discussion and conclusions

We have presented the analysis of pathological and sub-pathological changes in two samples of rabbit remains with a very different origin: modern domestic rabbits kept in captivity and archaeological remains from a naturally-accumulated rabbit population. The changes registered in each sample and their skeletal distribution, differ greatly. Sample 1 shows pododermatitis, a chronic infectious/inflammatory disease with associated hypervascularisation of the physes. The presence of musculoskeletal stress markers could also be a consequence of captivity, caused by the regular hind-limb thumping of anxious rabbits, or it could relate to the conformation of these animals. Certainly, the directional asymmetry in hind limb elements would be unlikely to occur outside of captive-bred population, although whether this relates to the selective breeding of these meat animals, adaptation to a behavioural response, or developmental instability, is uncertain. Combined, these characteristics allow us to speculate that conditions of upkeep, perhaps in combination with inherited characteristics, are responsible for the pathological and sub-pathological changes observed in Sample 1.

Sample 2 shows a very different lesion profile: the most significant pathology observed in the natural rabbit population was trauma. The other lesions present may not have significantly affected the health-status of the animals, and are known to have diverse causes, making it difficult to draw any conclusions regarding their presence.

We are aware that in the modern assemblage of rabbit remains skeletons were not complete and that it was not ideal for making comparisons because it was in essence a pre-selected sample exhibiting pathological and sub-pathological changes. For this reason, the prevalence data need to be interpreted with caution. However, what is clear from this study is that the prevalence of pathological and sub-pathological skeletal changes in the rabbits, and thus their health status, are closely related to living conditions. This is supported by the high percentage of affected bones in the domestic rabbit sample (21 %) compared with the naturally-accumulated assemblage of wild rabbits (1.7 %). The significantly lower proportion of pathological/sub-pathological bones in the Dudley Castle sample is unsurprising. It merits emphasis that the two assemblages are not directly comparable because of their markedly different element distribution (Table 2). Nevertheless, there are good reasons to expect a lower abundance of skeletal pathologies in a wild population. Firstly, injured rabbits or those with acute or even chronic illnesses are more susceptible to predation, and thus will not be incorporated into a naturally-accumulated assemblage. Secondly, because the likelihood of developing a skeletal lesion increases with age (e.g., Harris, 1979) and skeletal pathologies in a single individual are cumulative, animals with a short life-span are always more likely to exhibit lower lesion prevalence. Thirdly, morbidity will almost by definition differ between wild and domestic animals due to the higher risk of congenital pathologies in the genetically manipulated domestic form.

Based on the two samples considered in this study, we predict that intensively managed populations of rabbits will exhibit a higher prevalence of pathological and sub-pathological changes than that observed in the Dudley Castle assemblage. However, it is unlikely to attain the high frequency observed in the modern dataset, unless the element profile was significantly skewed towards particular body parts and because, the modern assemblage is in essence a pre-selected sample to have lesions and thus the lesion prevalence of 21 % should be interpreted with caution.

It is a familiar refrain in animal palaeopathological studies that more comparative datasets are required to establish the extent to which observed skeletal are typical of the assemblages from which they derive (e.g. Thomas and Grimm, 2011; Thomas and Johannsen, 2011), and this is equally pertinent here. Nevertheless, we hope to have demonstrated the value of systematically recording pathologies in rabbit bones, and the potential of such data for understanding interactions between rabbits and people in the past.

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