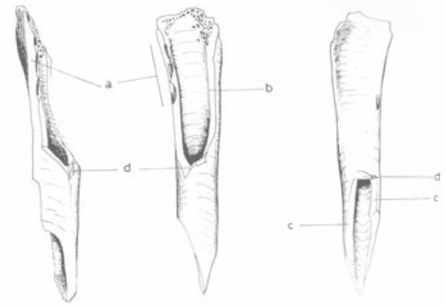

EARLY DEVELOPMENT OF THE EUROPEAN RABBIT (*ORYCTOLAGUS CUNICULUS* L. 1758): AN OSTEOMETRICAL TOOL TO ADDRESS TAPHONOMICAL AND ARCHAEOZOOLOGICAL ISSUES

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ABSTRACT:

The skeletal development of the European rabbit during its first weeks of life is a poorly documented phenomenon whose potential applications reach to various fields of research. In this paper a table is provided to turn the lengths of seven skeletal elements (mandible, humerus, radius, ischium, ilium, femur and tibia) into weight and age equivalents. The database consisted of sixteen rabbits of known size and weight from the same population whose ages were previously estimated through the application of widely used age-weight regression equations. This reference should allow faunal analysts to recognize those size thresholds for each element below which rabbits are not able to leave the burrow, a feature that will help spot them as intrusive elements in archaeological deposits.

Key words: *European rabbit,* Oryctolagus cuniculus*, early development, osteology, biometry, taphonomy, archaeozoology.*

1. INTRODUCTION

Small prey exploitation by hominines is a heated debate in prehistoric archaeology (Jones 2004; 2006; Lloveras *et al*. 2009). In the western Mediterranean region, and the Iberian peninsula in particular, this debate has been focused mostly on the role played by the European rabbit (*Oryctolagus cuniculus*, L.1758), a highly prolific, keystone species that constitutes one of the main prey items for a wealth of avian and mammalian predators (Corbet 1994; Delibes-Mateos *et al*. 2008; Wilson *et al*. 2016). Although the consensus nowadays concedes that rabbits were systematically preyed by Neanderthals prior to the arrival of Anatomically Modern Humans (AMH), the specificities of the phenomenon are still far from settled as of this writing (see Callou 2003 and Lloveras 2011, with references therein).

One major drawback that daunts the rabbit exploitation debate to this day has to do with the often taphonomically ambiguous nature that rabbit remains bear on archaeological deposits. Indeed, unlike most lagomorphs, rabbits are fossorial animals whose complex warrens and intricate system of galleries, are dug wherever soil conditions allow. It so happens that the often poorly or medium compacted sediments that archaeological deposits represent, both on sheltered and open-air sites, constitute optimal ground (literally!) for the activity of this animal. Once galleries are dug, all sorts of archaeological "mishappenings", from a mixing of materials to a collapse of levels, can take place in a stratified deposit. Still, due to the difficulty of detection during excavation, the most deleterious effect rabbit activities exert in archaeology is the intrusion of their bones into animal deposits from a previous time (Pelletier *et al*. 2017). Given the altricial (non-precocious) nature of newborn rabbits, animals from the youngest cohorts (i.e. age groups), with severely restricted mobility, stand the highest chances of dying or being trapped in their dens when galleries collapse or are flooded. For that reason, along with other potential signatures, checking for infantile and juvenile rabbits has become a routine for analysts looking for clues of intrusive animals in archaeological deposits (Pelletier *et al*. 2016; 2017). Although osteological studies exist that address rabbit age (Jones 2006), the few papers dealing with the first two weeks of life refer to the eruption of the upper and lower incisors in the cotton-tail rabbit, *Sylvilagus floridanus*, and the deciduous dentition replacement in the European rabbit (Dice and Dice 1941; Horowitz *et al*. 1973). How does one reliably recognize a young rabbit that could not leave its warren from another one that could? In other words, how small must a rabbit bone be to be sure that it represents an individual from the former but not the latter category? As things presently stand, we have essentially no data on the size of bones from rabbits during their first weeks of life. For that reason, the main goal of this paper is to provide data that will help fill this dearth of information.

2. EARLY DEVELOPMENT OF THE EUROPEAN RABBIT

Despite the crucial ecological role the European rabbit plays in Western Mediterranean terrestrial food webs and as invader into the regions where it was intentionally introduced, the details on its early somatic development are still wanting in their details. Corbet and Southern (1977) study on the British islands mention that wild newborn rabbit weight ranges between 30-35 g, yet Lockley (1965) working mostly in Wales, reports that newborns do not normally reach to two ounces (i.e. 56 g). In Australia newborn weight average reaches to 57 g, and increases at an approximate rate of 7,4 g per day, so that when animals emerge from the nest when 21 days old they weight about 185 g (Myers 1958). In the case of the domestic rabbit, in turn, Harant *et al*. (2001) record an average newborn weight of 79 g on a sample of 123 individuals. Other data suggest that when dry conditions prevail, all unweaned members of the population die, and the growth rates of recently weaned rabbits are markedly retarded (Soriguer and Rogers 1979; Rogers *et al*. 1994). Such large differences may probably reflect another important yet barely explored issue, namely that average newborn weight depends on factors such as the age of the female –who will give birth to lower weight offspring when breeding for the first time–, litter number –weight inversely correlating with the number of newborns–, and environmental variables having to do with the season of the year, climate, plant density and productivity, etc. In the case of the Iberian peninsula, the only mention to newborn weight are the seven wild specimens from which Soriguer developed his growth curve, whose values are nowhere specified (Soriguer 1980; 1981). Under such circumstances, it seems difficult to settle for a standard newborn weight, a range of 30-60 g being a probably much safer bet than any specific figure. What both Corbet and Southern (1977) and Lockley (1965) stress is that weight at birth essentially doubles during the first week of life. This growth rate also applies to domestic rabbits (Harant *et al.* 2001). Given that a linear growth rate has been detected for the first months of life in the species, that will bring the new range of weights to oscillate between 60-120 g during the first week of life, doubling during the second week when eyes become functional (10 days is the maximum estimate for this event, with 7-8 days representing the average) (Ferreira and Ferreira 2014). Corbet and Southern (1977) mention that the young first exit the warren on their 18th day of life, when average weight approaches 140 g, although these are short-lived excursions as the animals are still lactating. Females stop lactating around the start of the 4th week of life (most often from the 23th to the 25th day) when weight averages around 150 g (Corbet and Southern 1977). After the 4th week of life, when weight ranges between 250-300 g, rabbits start grazing during progressively more prolonged periods, becoming vulnerable to a wider range of predators. After the first month of life it appears that weight gains oscillate between 40-60 g per week. Taking these values as reference, weight gains during the ensuing ten weeks would range as follows:

5th week: 240-310 g
6th week: 280-370 g
7th week: 320-430 g
8th week: 360-490 g
9th week: 400-550 g
10th week: 440-610 g
11th week: 480-670 g
12th week: 520-730 g
13th week: 560-790 g
14th week: 600-850 g

Although original pooled data from males and females estimated a minimum weight for adult (i.e. mature) rabbits in southern Iberia to be 900 g (Soriguer 1981), that figure was later more accurately set at 1125 g for males and 1025 g for females (Arqués and Peiró 2005). These weights are essentially similar to those reached by rabbits (subspecies *O. c. cuniculus*) in Great Britain whose maximum weight ranges 1.2-2 kg although Callou (2003) records more marked weight differences between the two European subspecies [*O. c. cuniculus* (NE Spain and Northern Europe): 2 kg; *O. c. algirus* (SW Iberia): 1 kg]. One problem of restricting values to single figures is that these do not take into account the differences that exist, even in adults of similar age, depending on factors such as the condition and sex of the specimen, environmental productivity, density, etc. Although some works attempt to set apart biometric differences between subspecies from the effects of geography and sex, more research is needed since other factors should be considered (Ferreira *et al.* 2016). Indeed, given the large amount of phenotypic variability among present rabbit populations, this is a crucial aspect of any future research (Pelletier 2019).

To sum up, whereas the sources of variability for weights are not only age-dependent, most data refer to adult specimens, the evolution of weight during the early weeks of life being preciously scarce.

3. MATERIAL AND METHODS

For this study 16 non-adult rabbits, covering a weight range from 105-855 g, were studied. Although this is clearly a restricted sample, it nevertheless covers the weight range that corresponds with the fast growth period of rabbits from their first week of life until reaching maturity (14/15th week). This allows us to quantify weight increase with the somatic growth of the bones, expressed as linear measurements (once weight increase becomes stabilized around 800-900g, no possibility exists of establishing a reliable relationship between weight and age, measurements or others).

The specimens derive from a legal bagging operation ("saca") that took place on June 26th, 2016 on a collective hunting ground ("coto") near the town of Trescasas (Segovia, Spain: 40º 57' 36.21'' N, 4º 02' 16.42'' W). The location of Trescasas is interesting since it lies within the hypothetical NW-SE hybridization band that purportedly separates the subspecies of rabbits described for continental Europe. For such

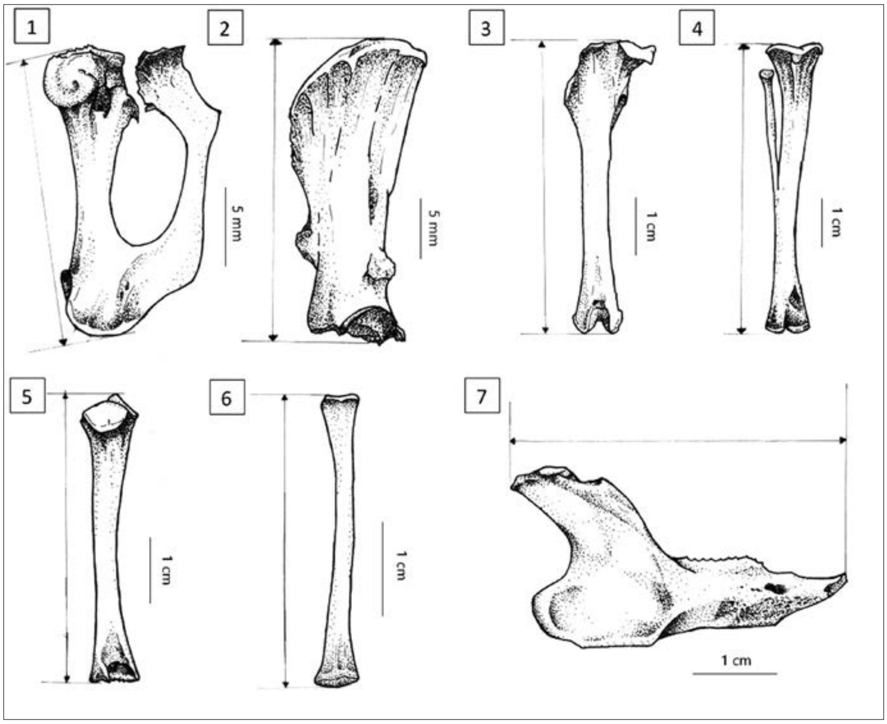

Fig. 1: Measuring points to record the greatest length (GL) of the Ischio-pubis (1), Ilium (2), Femur (3), Tibia (4), Humerus (5) and Mandible (7) and the diagonal length (LD) of the Radius (6). All elements shown are dextral in cranial (3, 4, 5, 6), ventro-lateral (1, 2) and lateral (labial) views (7). Illustrations by Daniel Marchena Pérez.

reason, a complementary goal of our research will aim at exploring how growth parameters from our sample, specifically weight, compare with those from published populations of *O. c. cuniculus* and *O. c. algirus* (work in progress).

A series of standard body measurements were taken in all specimens. These include "body" length (i.e. head+body), tail length, length of the right posterior foot and length of the right ear lobe. Still, the only corporal parameter deemed appropriate for our study was weight. Weight was taken in the laboratory on fresh specimens thus it is possible that some weight loss occurred between capture and recording. Although probably negligible (only specimens in fine condition not exhibiting bleeding or damage of any sort were selected), it is possible that weight values represent under-estimations this being a source of variation one needs to keep in mind when trying to establish cohorts.

Protocols carried after skeletonization included an evaluation of epiphyseal fusion and tooth replacement for each specimen along with the measurement of relevant bones. In addition to the mandible (skulls disintegrated during the skeletonization process), state of fusion was recorded on the most frequently retrieved limb bones (i.e. humerus, radius, femur and tibia) as well as the main ossification centres of the pelvis, namely the ilium and ischiopubic bones. Although the essentials of measuring follow Driesch (1976), working with diaphyses devoid of epiphyses called for a slight re-framing of the measuring points in the case of the appendicular elements and the inclusion of new measuring points for the pelvic elements. Although width and breadth were taken in all limb bones, in this paper we will only present data on the greatest linear measurement from each element. In the case of the mandible this would correspond with measurement 1 from Driesch (1976: fig. 25), and in the humerus, femur and tibia with the greatest length (GL) of the diaphysis (i.e. from the most proximal to the most distal point) (fig. 1, 3 to 1, 5). In the case of the greatest lengths of the pelvic bones, the measuring points are the most cranial and the most caudal prominences on each element (fig. 1, 1 and 1, 2), whereas the bending of the radius in young rabbits turns this length into more of a diagonal (DL) than a "straight" one (parallel to the main axis) (fig. 1, 6). One must remark that only unfused elements were considered for this study in order to make measurements comparable. In this way,

AMM sample		A		B		C		D		Estimated age AMM sample
		O. cuniculus algirus Portugal (Ferreira & Ferreira 2014)		*O. cuniculus algirus* Andalucía Occidental (Soriguer 1981)		*O. cuniculus cuniculus* England (Southern 1940)		*O. cuniculus cuniculus* Australia (Dunnet 1956)		
AMM no.	Weight (g)	Days	Months	Days	Months	Days	Months	Days	Months	
79	105	8.50	0.28	22.97	0.77	11.17	0.37	11.28	0.38	1- 1,5 week
78	140	14.15	0.47	30.56	1.02	14.83	0.49	14.86	0.50	1- 1,5 week
77	160	17.17	0.57	34.45	1.15	16.92	0.56	16.91	0.56	2 weeks
76	170	18.63	0.62	36.31	1.21	17.97	0.60	17.93	0.60	2 weeks
74	205	23.59	0.79	42.43	1.41	21.63	0.72	21.51	0.72	3 weeks
75	220	25.66	0.86	44.92	1.50	23.20	0.77	23.05	0.77	3 weeks
73	225	26.34	0.88	45.73	1.52	23.72	0.79	23.56	0.79	3 weeks
71	235	27.70	0.92	47.34	1.58	24.77	0.83	24.58	0.82	3 weeks
72	255	30.39	1.01	50.49	1.68	26.86	0.90	26.63	0.89	3-4 weeks
68	270	32.39	1.08	52.80	1.76	28.43	0.95	28.16	0.94	3-4 weeks
70	310	37.68	1.26	58.78	1.96	32.61	1.09	32.26	1.08	3-4 weeks
67	315	38.34	1.28	59.51	1.98	33.14	1.10	32.77	1.09	3-4 weeks
69	345	42.30	1.41	63.86	2.13	36.28	1.21	35.84	1.19	1 month
66	560	72.53	2.42	94.83	3.16	58.76	1.96	57.85	1.93	2 months
65	625	83.08	2.77	104.89	3.50	65.56	2.19	64.50	2.15	2-3 months
64	855	134.80	4.49	149.62	4.99	89.62	2.99	88.04	2.93	> 3 months

Fig. 2: Diagonal length (Radius) and greatest length (all remaining elements) in millimeters of the specimens (identified by weight) analyzed for this study. [(-): not available; (F): element featuring fusion of some ossification centres)]. For specimen code see Figure 4.

when an element exhibited a partial or total fusion of one of its epiphyseal centers it was not measured. Measurements were taken with a Mitutoyo digital caliper whose reading error is +/- 0.01mm. Although enzyme activity during skeletonization can wear away the growth plate of appendicular bones, this wearing was deemed negligible. Still, in order to neutralize for that contingency, we considered that the error implicit in our measurements was never below +/- 0.1 mm.

Since the age of our specimens was unknown, we used age-weight tables and formulae available for rabbit populations from England, Australia, Southern Spain and Portugal given the good correlation existing between both parameters (Dunnet 1956; Ferreira and Ferreira 2014; Soriguer 1981; Southern 1940). The equations for estimating age from weight data appear in Figure 3. Once this was done, weight of our specimens was correlated with each of the seven linear measurements selected for analysis. This correlation was developed through linear regression equations established between a given specimen's weight and the osteometrical values of each of its seven elements. Only dextral elements were used for this purpose. When these were missing, the left element was taken. Because weight shows an exponential growth when compared with bone growth, both variables of the regression were logarithmically transformed so that their relationship could be expressed as a linear model.

Correlation between variables was tested with Pearson's correlation coefficient using the "R" package (v. 3.6.1; R Core Team 2019), thus was simultaneously represented as graphs. A 95% confidence interval and the range of possible predictions were also estimated.

4. RESULTS AND DISCUSSION

Figure 2 provides the individual measurements of the studied elements for each specimen. Incorporating their weights in the table allows for a preliminary overview, however coarse, of visualizing how bone growth correlates with corporal development. In this way, figure 2 constitutes a preliminary tool to infer weight from osteometric data during the early development of the rabbit. As can be seen on the humerus, fusion of the distal epiphysis starts with specimen AMM66 (560 g), whose dextral trochlea is partially fused (+/-) though not its parasagittal equivalent. It appears that humeral trochleae would be fully fused above 600 g as our two specimens above this threshold evidence (AMM65: 625 g; AMM64: 855 g). The latter specimen additionally exhibits full fusion of the proximal epiphyses of the radius and the pelvic bones; all remaining fusion centres on our samples remain unfused. Although the fusion of the ilium and the ischio-pubis on specimen AMM64 may suggest that this individual might have been able to gestate from a strictly biomechanical standpoint (i.e. it might be either mature or reaching maturity, when skeletal development levels off), its weight falls well below the +1 kg sexual maturity threshold reported for Iberian rabbits (Arqués and Peiró 2005).

A *t*= log↓0,6 (log↓0,03 (*W*/ 1125))	**B** *t*= [ln(√3&1−*w*/1,069)]↑3 / −0,01596 +38,57
C *t*=0,529+102,35 *W*	**D** *t*=0,188+104,06 *W*

Fig. 3: Equations for estimating age (t) in rabbits from weight values (W). [(A): Fereira & Ferreira (2014); (B) Soriguer (1981); (C) Southern (1940); (D) Dunnet (1959)].

The application of the age-weight regression equations (fig. 2) on our weight data provided an additional way to infer the age of our specimens (fig. 3; fig 4). One first issue to remark are the rather striking differences in age values for any given weight depending on the equation used. This should come as no surprise given the multiple sources of variation affecting growth and the fact that none of them were taken into account when the equations were developed (Dunnet 1956; Ferreira and Ferreira 2014; Soriguer 1981; Southern 1940). In other words, the data on which the equations were based are not standardized. Also evident is that the differences of the age estimations are larger in the smallest specimens and smaller in the largest ones. This might explain why the smallest of our specimens in terms of the osteometry of several elements (AMM78) is *ca.* 40% heavier than the lightest one (AMM79) (fig. 2). Still, although development may start with rather different weight differences at birth and proceed faster or slower during this period of "exponential" pre-maturation growth depending on the circumstances, it appears that rabbits tend to converge on a given weight (rather weight range) upon reaching maturity. This makes perfect biological sense since below a certain weight it seems probable that the reproductive effort could be compromised.

Independently of these biological considerations, it seems that the southern Spanish population studied by Soriguer (1981) at Coto de Doñana

Weight	Femur		Tibia		Ischium		Ilium		Humerus		Radius		Mandible	
	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left
855 g	60.89	60.95	69.17	68.98	27.49	27.53	29.37	29.38	F	F	F	F	44.19	-
625 g	57.04	57.3	63.69	63.74	24.86	24.96	26.62	26.62	F	F	38.72	38.72	42.7	42.97
560 g	53.23	53.14	57.52	57.48	24.35	24.51	25.69	26	F	41.26	35.06	35.34	41.75	-
345 g	-	44.64	-	47.43	19.57	19.53	20.92	21.94	34.52	34.44	-	28.71	-	-
310 g	-	-	48.79	48.96	-	19.8	21.78	21.59	-	34.86	30.75	-	35.49	35.38
255 g	44.53	44.55	48.89	48.77	19.28	19.32	22.29	-	33.23	34.01	30.15	30.47	-	-
270 g	39.37	39.26	43.62	43.56	16.97	17.28	20.01	19.95	30.89	31.18	25.94	26.35	-	-
315 g	41.35	41.73	-	45.29	17.7	-	-	-	-	32.29	-	28.47	-	34.73
235 g	35.55	35.9	39.69	39.35	16.13	16.08	17.67	17.99	28.79	28.89	24.64	24.91	-	31.49
225 g	32.25	32.47	36.08	36.35	14.67	14.72	16.21	16.23	27.09	27.13	23.45	23.38	-	29.06
220 g	37.97	37.52	42.15	42.11	-	17.01	-	19.09	-	30.56	-	-	-	33.03
205 g	38.54	38.54	40.85	40.98	15.91	15.92	18.5	18.81	31.36	-	25.67	-	32.76	32.61
170 g	33.04	33.35	36.63	36.16	14.69	15.13	16.47	16.31	26.03	26.89	22.76	23.17	29.64	29.64
160 g	-	32.35	35.17	35.08	14.29	-	15.37	15.34	25.27	24.98	22.31	22.18	-	-
105 g	-	-	-	-	-	11.8	12.42	-	-	21.52	-	-	-	-
140 g	-	24	27.12	26.98	10.25	10.46	11.71	11.77	20.58	20.61	18.03	18.07	25.92	25.8

Fig. 4: Age estimation of specimens (AMM) through weight data applying the equations from Soriguer (1981), Ferreira & Ferreira (2014), Southern (1940) and Dunnet (1959) (see figure 3).

is the outlier on this age-weight table. And its differences do not make much sense. In this way, one of our smallest specimens (AMM79), certified to be on its first week of life by three of the equations that set its age between 9-11 days (fig. 4), would, according to Soriguer (1981), be instead 23 days old (i.e. non-lactating). This seems baffling given that most of the small rabbits could barely move when forced out of the warren, thus were probably still lactating (N. Batuecas, verb. com.). For such reason, we refrained from using Soriguer's estimations and turned instead to the pooled average of ages based on the remaining equations. These age inferences are provided in the final column on figure 4 and evidence that the age range we are dealing with here would run roughly from the end of the first week to the fourth or perhaps fifth month of life (fig. 4).

The correlation of weight with the selected osteometrical parameters yielded high correlation coefficients (r^2) in all seven instances (i.e. no single value below 0.87). The regression equations that allow weight (fig. 5), and eventually age, to be inferred from the lengths of these seven elements are as follows (W = weight):

Ischium: $\ln(W) = 2{,}0163 \times \ln(IS_{(GL)}) - 0{,}1538$ (r^2= 0,9018)
Ilium: $\ln(W) = 2{,}0506 \times \ln(IL_{(GL)}) - 0{,}4728$ (r^2= 0,8859)
Humerus: $\ln(W) = 2{,}0781 \times \ln(H_{(GL)}) - 1{,}5724$ (r^2 = 0,8897)
Radius: $\ln(W) = 2{,}0706 \times \ln(R_{(DL)}) - 1{,}2228$ (r^2= 0,887)
Femur: $\ln(W) = 1{,}9978 \times \ln(F_{(GL)}) - 1{,}7211$ (r^2 = 0,8766)
Tibia: $\ln(W) = 2{,}0257 \times \ln(T_{(GL)}) - 2{,}0280$ (r^2 = 0,8999)
Mandible: $\ln(W) = 3{,}2561 \times \ln(M_{(GL)}) - 0{,}4728$ (r^2= 0,9276)

As can be seen in figure 5, not all elements feature similar growth rates, completing growth at different times. In particular, the data show that the main elements of the forelimb (humerus and radius) have their epiphyses fusing at far lower weights than their hindlimb equivalents, reaching growth plate senescence earlier (none of the femora nor the tibiae in our sample had their epiphyses fused to the diaphysis). These differences in ossification times conform with the data provided in previous works (Heikel 1959; Taylor 1959). This fact alone indicates that the hindlimb of the rabbit, essential for its peculiar mode of locomotion, keeps on growing for a far longer time than the markedly shorter forelimb. Unless skeletons are found complete, other factors being equal, the implications of these differences when translated into age groups suggest that forelimb elements may provide a biased age profile of archaeological populations, allotting as reproductive (mature) individuals below their reproductive age.

Keeping in mind that weight increase in relation to the increase in length of any given element is smaller in bones whose length range is wider, it can be said that the reliability of the weight estimation will be higher if there is a minor variation of the weight when length increases. In other words, the effect of the error is minimized, so there is a higher variation in the length with the same weight increase. In this way, despite not scoring the highest r^2 values, the best predictors of weight in young rabbits would be the tibia and the femur

In order to provide a preliminary correspondence between our data and archaeological samples, we have defined five cohorts of non-mature rabbits based on their weight and biometrical values (fig. 6; fig. 7). Each cohort features non-overlapping corporal parameters in terms of weight and bone size, as well as non-arbitrary biological landmarks, namely:

1. Newborn (cohort I; approx. first week of life: eyes closed)
2. Infantile (II; after first week of life: eyes open but still lactating)
3. Juvenile (III; second half of the first month of life: grazing starts)
4. Juvenile/subadult (IV; second and third months of life: animals venture outside of the warren during prolonged periods of time)
5. Subadult (V; above three months of life: non-mature but otherwise behaving as an adult)

In principle, and from the standpoint of the archaeozoologist, newborns and infantile specimens would be difficult to capture except for predators venturing into the warren. For such reason, these would be the best markers to reveal the contamination of an archaeological deposit by rabbits. Juveniles could be preyed by a wealth of raptors and carnivores but very unlikely by people unless ferreting beasts were used. Their presence in an archaeological deposit would call in most cases for a taphonomical analysis to determine the collecting agent(s). Members of cohort IV are reaching a size that makes them

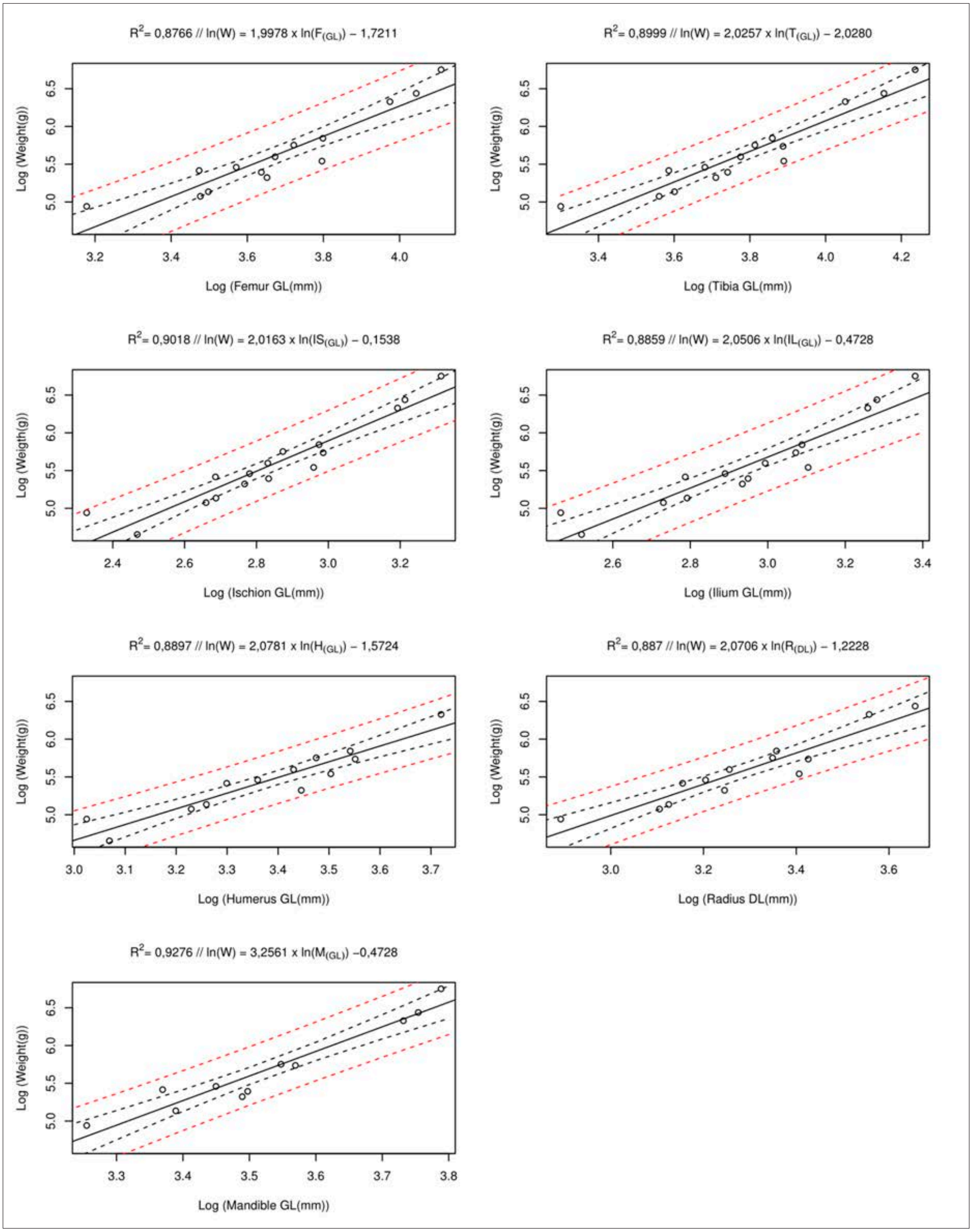

Fig. 5: Regression line and correlation equation of the natural logarithmic transformation of weight on the lengths of selected elements (continuous line). The 95% interval of confidence is represented by the dashed inner line and the prediction intervals by the dashed outer line.

SKELETAL ELEMENT		Mandible			Humerus			Radius		
Weight range	Cohort	n	Range	ȳ	n	Range	ȳ	n	Range	ȳ
855g	V	1	44	-	-	-	-	-	-	-
625g	IV	2	42.7-42.9	42.8	-	-	-	2	38.7	38.7
560g	IV	1	41.7	-	1	41.2	-	2	35-35.3	35.2
255-345g	III	3	34.7-35.5	35.2	8	30.8-34.8	33	7	26-30.7	28.7
160-235g	II	7	29-33	31	10	25-31.3	27.7	9	22.2-25.6	23.6
105-140g	I	2	25.8-25.9	25.85	3	20.6-21.5	21	2	18.03-18.07	18

Fig. 6: Weight and biometry values of the mandible, humerus and radius for the pre-reproductive cohorts of the European rabbit (*Oryctolagus cuniculus*, L.) defined in this paper.

SKELETAL ELEMENT		Ischion			Ilion			Femur			Tibia		
Weight range	Cohort	n	Range	ȳ	n	Range	ȳ	n	Range	ȳ	n	Range	ȳ
855g	V	2	27.4-27.5	27.5	2	29.3	29.3	2	60.8-60.9	60.85	2	69-69.1	69.05
625g	IV	2	24.8-24.9	25	2	26.6	26.6	2	57-57.3	57.2	2	63.6-63.7	63.65
560g	IV	2	24.3-24.5	24.4	2	25.6-26	25.8	2	53.1-53.2	53	2	57.4-57.5	57.45
255-345g	III	8	16,9-19.5	18.7	7	20-22.2	21.2	7	39.2-44-6	47.2	8	43.5-48.9	47
160-235g	II	10	14.3-17	15.4	11	15.3-19	17	11	32.3-38.5	35.2	12	35-42	38.4
105-140g	I	3	10.2-11.8	10.8	3	11.7-12.4	12	1	24	-	2	26.9-27.1	27

Fig. 7: Weight and biometry values of the ischium, ilium, femur and tibia for the pre-reproductive cohorts of the European rabbit (*Oryctolagus cuniculus*, L.) defined in this paper.

more attractive to human hunters, the lower energy intake they represent being more than compensated for by their inexperience, thus the facility to hunt them. Still, presence of cohort IV individuals, when monopolistic, would require work to elucidate the nature of the collecting agent. Lastly, subadults could be considered, for all practical (hunting) purposes, regular prey items for humans.

5. CONCLUSSIONS

Despite the numerous questions that the study of very young animals (newborns and even foetuses), raises for addressing a wealth of archaeological issues, the study of these cohorts has, as of this writing, lagged behind that of adults. Lack of reference collections and higher chances of their remains being lost in deposits when these are improperly excavated may explain such a state of affairs but are definitively not the sole reason for this systematic neglect. The data presented in this paper are interesting and contentious, and further work along these lines is needed to substantiate and refine proposals such as the five cohorts of non-mature rabbits. In addition, further work is needed to test the validity of the weight/age/size correlations in more populations and to refine the assignment of age based on biometrical parameters. We therefore conclude by stating that we hope our paper will help pave the way to a more systematic study of very young animal remains in a not too distant future.

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REFERENCES

ARQUÉS, J.; PEIRÓ, V. (2005): Estructura de sexos y edades de una población de co-nejos (Oryctolagus cuniculus) del sudeste de España, *Mediterránea, Serie de Estudios Biológicos*, Época II, 8-33. DOI: https://doi.org/10.14198/MDTRRA2005.18.10

CALLOU, C. (2003): *De la Garenne au Clapier: étude Archéozoologique du Lapin en Europe occidentale*, Paris.

CORBET, G. B. (1994): Taxonomy and origins, *The European rabbit: The History and Biology of a successful colonizer* (H. V. Thompson, C. M. King, eds.), Oxford, 1-7.

CORBET, G. B.; SOUTHERN, H. N. (1977): *The Handbook of British Mammals*. 2nd edition, Oxford.

DELIBES-MATEOS, M.; DELIBES, M.; FERRERAS, P.; VILLAFUERTE, R. (2008): Key role of European rabbits in the conservation of the Western Mediterranean basin hotspot, *Conservation Biology* 22 (5), 1106-1117.
DOI:https://doi.org/10.1111/j.1523-1739.2008.00993.x

DICE, L. R.; DICE, D. S. (1941): Age changes in the teeth of the cottontail rabbit, *Sylvilagus floridanu*s, *Papers of the Michigan Academy of Sciences, Arts & Letters* 26, 219-228.

DRIESCH, A. VON DEN (1976): *A Guide to the Measurement of Animal bones from Archaeological Sites*, Peabody Museum Bulletin, no.1, Cambridge.

DUNNET, G. M. (1956): Growth Rate of Young Rabbits, *Oryctolagus cuniculus* (L.), *CSIRO Wildlife Research* 1 (1), 66-67.
DOI: https://doi.org/10.1071/CWR9560066

FERREIRA, A.; FERREIRA, A. J. (2014): Post-weaning growth of endemic Iberian wild rabbit subspecies, *Oryctolagus cuniculus algirus*, kept in a semi-extensive enclosure: implications for management and conservation, *World Rabbit Science* 22 (2), 129-136.
DOI: https://doi.org/10.4995/wrs.2014.1673

HARANT, H.; PORZIG, R.; THIELEBEIN, J.; SAAR, W.; SCHULER, L. (2001): Development of body weight in rabbits (*Oryctolagus cuniculus*) after embryo transfer of reciprocal nuclear combinations to a neutral line of recipients, *Archiv für Tierzucht-Archives of Animal Breeding* 44(1), 71-88.

HEIKEL, H. V. (1959): On ossification and growth of certain bones of the rabbit; with a comparison of the skeletal age in the rabbit and in man, *Acta Orthopaedica Scandinavica* 29 (14), 171-184.
DOI: https://doi.org/10.3109/17453675908988796

HOROWITZ, S. L.; WEISBROTH, S. H.; SCHER, S. (1973): Deciduous dentition in the rabbit (Oryctolagus cuniculus): A roentgenographic study, Archives of oral biology 18(4), 517-523.
DOI: https://doi.org/10.1016/0003-9969(73)90072-1

JONES, E. L. (2004): *Broad-spectrum diets and the European rabbit (*Oryctolagus cuniculus*): Dietary change during the Pleistocene-Holocene transition in the Dordogne, southwestern France*, Unpublished PhD thesis. University of Washington. Washington.

JONES, E. L. (2006): Prey Choice, Mass Collecting, and the Wild European Rabbit (*Oryctolagus cuniculus*), *Journal of Anthropological Archaeology* 25 (3), 275-289.
DOI: https://doi.org/10.1016/j.jaa.2005.11.002

LOCKLEY, R. M. (1965): *The private life of the rabbit*, London.

LLOVERAS, L.; MORENO-GARCÍA, M.; NADAL, J. (2009): Butchery, cooking and human consumption marks on rabbit (*Oryctolagus cuniculus*) bones: an experimental study, *Journal of Taphonomy* 7 (2), 179-201.

LLOVERAS, L. (2011): *Análisis tafonómicos de restos de lepóridos consumidos por carnívoros terrestres y aves rapaces. Aplicación al estudio de restos arqueológicos del Pleistoceno y Holoceno de la Península Ibérica*, Unpublished PhD thesis. Universitat de Barcelona. Barcelona.

MYERS, K. (1958): Further observations on the use of field enclosures for the study of the wild rabbit, *Oryctolagus cuniculus* (L.), *CSIRO Wildlife Research* 3(1), 40-49.
DOI: https://doi.org/10.1071/CWR9580040

PELLETIER, M. (2019): Morphological diversity of wild rabbit populations: implications for archaeology and palaeontology, *Biological Journal of the Linnean Society* 128 (1), 211-224.
DOI: https://doi.org/10.1093/biolinnean/blz074

PELLETIER, M.; BRUGAL, J. P.; COCHARD, D.; LENOBLE, A.; MALLYE, J. B.; ROYER, A. (2016): Identifying fossil rabbit warrens: Insights from a taphonomical analysis of a modern warren, *Journal of Archaeological Science*: Reports 10, 331-344.
DOI: https://doi.org/10.1016/j.jasrep.2016.10.016

PELLETIER, M.; ROYER, A.; HOLLIDAY, T. W.; DISCAMPS, E.; MADELAINE, S.; MAUREILLE, B. (2017): Rabbits in the Grave! Consequences of Bioturbation on the Neandertal "burial" at Regourdou (Montignac-Sur-Vézère, Dordogne), *Journal of Human Evolution* 110, 1-17.
DOI: https://doi.org/10.1016/j.jhevol.2017.04.001

R CORE TEAM 2019. R: *A language and environment for statistical computing*, R Foundation for Statistical Computing, Vienna, Austria. [https://www.R-project.org/].

ROGERS, P.; SORIGUER, R.; ARTHUR, C. M. (1994): The rabbit in continental Europe, *The European wild rabbit: the history of a successful colonizer* (H. Thompson, C. M. King, eds.), Oxford University Press, 22-63.

SORIGUER, R. C. (1980): El Conejo, *Oryctolagus cuniculus* (L.), en Andalucía Occidental: Parámetros Corporales y curva de Crecimiento, *Doñana Acta Vertebrata* 7 (1), 83-90.

SORIGUER, R. C. (1981): Biología y dinámica de una población de conejos (*Oryctolagus cuniculus*, L.) en Andalucía Occidental, *Doñana Acta Vertebrata* 7-8, 1-318.

SORIGUER, R. C.; ROGERS, P. M. (1981): The European wild rabbit in Mediterranean Spain, *Proceedings of the world lagomorph conference* (K. Myers, C. D. Macinnes, eds.), Guelph, 600-613.

SOUTHERN, H. N. (1940): The ecology and population dynamics of the wild rabbit (*Oryctolagus cuniculus*), *Annals of Applied Biology* 27 (4), 509-526.

TAYLOR, R. H. (1959): Age Determination in Wild Rabbits, *Nature* 184 (4693), 1158. DOI: https://doi.org/10.2307/2402516

WILSON, D. E.; LACHER, T. E. Jr; MITTERMEIER, R. A. (eds.) (2016): *Handbook of the Mammals of the World. Volume 6. Lagomorphs and Rodents I*, Barcelona.