Quaternary International xxx (2011) 1–10

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Biostratinomy applied to the interpretation of scavenger activity in paleoecosystems

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ARTICLE INFO

Article history:
Available online xxx

ABSTRACT

Palaeontological sites can be a significant sample of the palaeocommunity to which they belonged, or represent effects of animal consumption. A general methodological study has been designed to contrast the pre-depositional characteristics of any anthropological or natural thanatocenosis and taphocoenosis/oryctocoenosis. A biostratinomic study of the carcass association scattered throughout Doñana Biological Reserve (Huelva, Spain) was performed to determine whether there are general patterns that can be applied to the taphonomic study of archaeological/palaeontological sites. All these results have shown that palaeobiological interpretations need biostratinomical studies to interpret the past, and this work has presented the analyses of an organic deposit in a natural ecosystem. The differences with other ecosystems located in different latitudes remain to be determined in order to define a general model to explain the formation of bone assemblages. The main objective of this paper is to apply the biostratinomic results of the Doñana Biological Reserve (DBR), an example of a Mediterranean ecosystem, in the interpretation of Venta Micena, a paleontological Early Pleistocene site located inOrce (Granada, Spain).

1. Introduction

There are numerous studies on vertebrate taphonomy (Blumenschine, 1986; Kidwell and Behrensmeyer, 1988; Mondini, 2000; Domínguez-Rodrigo, 2001; Ioannidou, 2003; Pasda, 2005; Montalvo et al., 2007; Muñoz et al., 2008; Gal, 2009). However, few researchers analyze the general patterns of carcasses preservation produced by living populations applied to the reconstruction of ancient communities (Western and Behrensmeyer, 2009).

Behrensmeyer and Boaz (1980)characterized the deposits of carcasses in a natural ecosystem produced by carnivore-scavenger activity in Amboseli National Park, calculating the frequency of the carcasses located in relation with the total number of deaths occurring in a year (Western, 1980). This relationship was called the fossil potential of a community.

In 1990, Doñana Biological Reserve (Huelva, Spain) was a natural area undergoing study. Not only were the turnoverrates of most vertebrate species unknown, but also there was no control over the number of deaths so that the scavenging activity could be calculated. At that time, it was not possible to determine the fossil potential of the vertebrate community in Doñana with the method used in Amboseli. However, scavenging activity could be quantified by measuring another kind of loss of biological information, which is known as fossil potentiality (Bernáldez Sánchez, 2009). This concept relates the state of preservation of the body and the average time spent since the death of the animal. This relation has been measured in 24 bodies of six mammal species over 5 kg in mass. The results determined the dynamics of conservation of 17 carcasses (difficulties occurred finishing the monitoring of the other seven carcasses) under environmental conditions in Doñana, which were used to estimate the representation of a vertebrate community in the thanatocenosis, species by species, depending on the average time a carcass spent on the surface.

The study mentioned above was published by Bernáldez Sánchez (2009), and extended to other ecosystems in Bernáldez Sánchez et al. (2008). This paper sets out to apply the carcass destruction patterns and other observations made about the "Ecology of Death" in Doñana to the interpretation of the structure and composition of oryctocoenosis at Plio-Pleistocene sites in Southern Iberia.

This first interpretation focuses on the site of Venta Micena, inOrce (Granada, Spain), dated to 1.5–1.6 Ma by Martínez-Navarro (1991) and 1.3–1.1 Maby Arribas and Palmqvist (1999). The motivation was given by Martínez-Navarro (1991: 8) when he acknowledged the absence of studies of modern and fossil ecosystems located in similar latitudes to Venta Micena. At that time, the only examples of this kind of study had been made in tropical regions (Andrews et al., 1979).

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doi:10.1016/j.quaint.2011.06.023

Between the community and the association of buried elements, a phase may exist for which the total and partial loss of the biological information provided by carcasses, owing to the activity of the carnivores and scavengers in the community, can be quantified. The objective of the biostratinomic study of mammals in the Doñana Biological Reserve was to determine the patterns of destruction and conservation of the carcasses deposited on the surface of an ecosystem in the Mediterranean basin. The results were inferred in the methodology of the study and in the interpretation of anthropic deposits associated with Holocene archaeological sites (Bernáldez Sánchez, 2009, 2002a) and paleontological sites from the southern Iberian Peninsula.

2. Study area: Doñana biological reserve (DBR)

The biostratinomic study of the mammals in Doñana Biological Reserve was carried out between November 1988 and April 1991 (Fig. 1). This location has the highest faunal diversity in the Mediterranean basin (Soriguer et al., 2001), allowing the possibility of relating the diversity of biotopes with the formation of carcass assemblage.

Doñana Biological Reserve has an area of 7600 ha, a Mediterranean climate with Atlantic influences, and three main ecosystems: *Marismas* (salt-marshes), *Monte* (scrublands) and *Dunas* (dunes). A fourth smaller unit or ecosystem is the ecotone between the *Marismas* and *Monte*, known as *Vera*. *Vera* is important because of the high productivity associated with its faunal richness (Soriguer, 1983, 1988,). Some 6.3% of the total reserve is occupied by *Marisma*, 86% by *Monte*, 3.5% by *Vera* and 4% by *Dunas* (Alés, 1987). Within these ecosystems, 12 biotopes were sampled, corresponding to open and covered areas (Table 1).

In terms of the abiotic conditions, the salt-marshes and the dunes are the most unstable units. The salt-marshes periodically experience flooding by the Guadalquivir River, which deposits thick layers of sediments, and the dunes are mobile units where water and wind destabilize the substrate causing bodies to be buried and unburied. In contrast, the scrublands (*Monte Negro* and *Monte Blanco*) and *Vera* are more stable ecosystems. In these areas, the carcasses remain on the surface without any geological effects, and any change is usually due to biotic activity (Fig. 2). Nevertheless, in *Vera* some small streams rising from the substrate (*caños*) are filled with some bone remains in times of drought.

The faunal richness in the Reserve in 1992 was determined by different authors, reporting 279 vertebrate species, with 7 fish species, 10 amphibians, 22 reptiles, 208 birds, and 32 mammals (Valverde, 1967; Delibes andBeltrán, 1986; Delibes, inpress). At that time, there were few scientific papers on the population dynamics in Doñana, so the necessary information was drawn from the Ph.D. theses that were then being carried out. These studies analysed the circumstances in which population sizes fluctuated due to seasonal factors, such as death after mating (red deer) or flooding, and occasional cases, such as illness (a plague affected the wild boar population in 1987) and droughts (an epidemic of botulism killed over 25,000 birds in 1989). These facts would explain certain biostratinomic results.

3. Materials and methodology

Between February 1989 and October 1990, 13.9 km^2 were sampled (18.3% of the total area of the Doñana Biological Reserve) in strips of 300 × 600 m and 300 × 100 m (Tellería, 1986), depending on the vegetation, during 50 days. The bone assemblages located consisted of 150 vertebrate carcasses in different states of destruction, belonging to 13 species: 2 reptiles (*Natrix natrix* and *Testudo graeca*), 2 birds (*Ciconia ciconia* and *Anser anser*) and 9 mammals (Table 2).

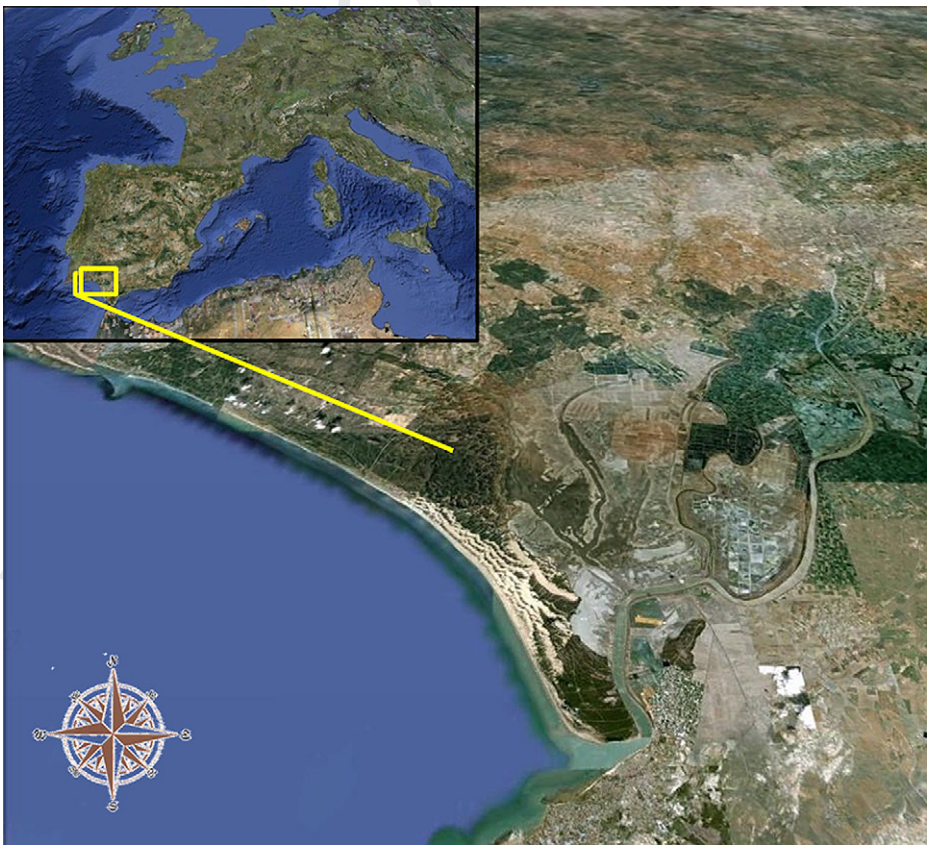

Fig. 1. Location of Doñana Biological Reserve in the Southern Iberian Peninsula (Huelva, Spain). Source: Google Maps.

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Table 1
This table shows the results obtained in the sampling of 12 biotopes in Doñana Biological Reserve (Huelva. Spain). MNI is the minimal number of individuals of the thanatocenosis; MNI/km^2 is the minimal number of individuals per square kilometre; FC is the frequency of carcasses and NSP is the number of species.

Ecosystems	Biotopes	Area (km^2)	MNI	FC	MNI/km^2	NSP
White scrubland	Cork-oaks	0.20	12	0.085	60.00	6
	Pine-wood "La Porquera"	0.03	1	0.007	33.33	1
	Lake "La Plancha"	0.03	3	0.021	100.00	3
	Lake "La Porquera"	0.03	2	0.014	66.67	1
	Lake "La Sanguijuela"	0.03	0	0.000	0.00	0
	Scrubland	6.21	19	0.133	3.38	5
Black scrubland	Scrubland "Nave del Muerto"	0.18	2	0.014	11.11	2
	Scrubland	0.43	0	0.000	0.00	0
Vera (ecotone)	Cork-oaks	1.02	47	0.331	46.08	8
	Pastures	4.98	48	0.338	9.64	7
Marshes	Rushland	0.60	5	0.035	8.33	3
Dunes	Perilagunar area	0.18	3	0.021	16.67	2
Total DBR	–	13.92	142	1	10.22	8

Nevertheless, this study only considered the statistical relationship (Spearman correlation) between the bone assemblages from 141 individuals of 8 mammal species with body mass between 1 kg and over 400 kg and the mammal population of Doñana (without considering the carcass of an introduced camel).

In order to estimate the date of death of the bodies, 24 carcasses of six mammal species were monitored between November 1988 and April 1991: 7 cows (*Bos taurus*), 3 horses (*Equus caballus*), 5 red deer (*Cervus elaphus hispanicus*), 3 fallow deer (*Dama dama*), 5 wild boars (*Sus scrofa*) and 1 fox (*Vulpes vulpes*). The objective was to analyze the port-mortem processes:

(1) disarticulation, measured by the number of connected bones (*NBc*);
(2) loss of bones, the percentage of bones preserved on the surface at a certain time. This variable is measured by the Skeletal Conservation Index ($SCI = NB\ x\ 10^2/NS\ x$ MNI, where NB is the number of bones recorded, NS is the total number of bones of the animal, and MNI is the minimal number of individuals), and
(3) dispersion area of the bones.

All these variables were transformed into the "bone loss rate"[$p = (\text{NS-NB})\ x\ 10^2/\text{NS}\ x\ t$; where t is the time between each control], "disarticulation rate"[$d = (\text{NS-NBc})\ x\ 10^2/\text{NS}\ x\ t$], and

Fig. 2. Dead cow in winter 1989 in *Vera*, the ecotone between the wetlands and the scrubland. Photo by E. Bernáldez Sánchez.

Table 2
List of mammal species sampled in Doñana Biological Reserve. MNI is the minimal number of individuals; NLI is the number of living individuals; FC is the frequency of carcasses and FL is the frequency of living individuals (all these values are for 1990). In this community, rabbit is the most abundant species, but is poorly represented in the thanatocenosis.

Species	Mass (kg)	MNI	FC	NLI	FL	Log (FC × 100/FL)
Camellus dromedarius[a]	>1.000	1	0.007	1	0.00006	–
Bos taurus	>400	31	0.220	170	0.010	3.32
Equus caballus	>300	11	0.080	25	0.002	3.70
Cervus elaphus	100	22	0.150	350	0.020	2.86
Dama dama	65	36	0.250	500	0.030	2.92
Sus scrofa	54	31	0.220	223	0.010	3.20
Vulpes vulpes	5	5	0.040	100	0.060	2.76
Herpestes ichneumon	5	1	0.007	152	0.0098	2.48
Oryctolagus cuniculus	1	4	0.030	14.740	0.910	0.49
TOTAL	–	142	–	16.261	–	–

[a] This species is not considered in the data analysis because it was an introduced camel.

"dispersion rate"[$s = (S_i–S_0)\ x\ 10^2/S_m\ x\ t$; where $S_i–S_0$ is the percentage increase in surface scattering of bones and S_m is the maximum area of dispersion recorded in the follow-up time].

The results were applied in estimating the age of Doñana's bone assemblages (sampled between February 1989 and October 1990) and the Pleistocene paleontological bone assemblages of Venta Micena (Granada, Spain).

4. Results

4.1. Doñana's thanatocenosis: composition and structure

In Amboseli National Park in Kenya, Behrensmeyer and Boaz (1980) concluded that all the species over 50 kg were present in the thanatocenosis, but the relative number of carcasses of the ungulate species recorded in the bone assemblages did not reflect the estimated population sizes in the censuses that had been made (Western, 1980). The bodies of individuals over 100 kg were over-represented, whereas the carcasses of individuals between 15 and 100 kg appeared with smaller frequencies than was expected. This effect was the result of selective annual carnivore–scavenger activity.

Restricting the biostratinomic study to the mammals (141 individuals, 94% of the 150 carcasses), the smaller and more numerous living species were not more frequent in the thanatocenosis than those of greater body mass (Table 2) despite their population size being greater. The relationship between the frequencies of carcasses and living individuals of the eight mammal species (1–400 kg) was significantly linked to the body mass($p = 0.005$; Rho = 0.874; g.l. = 7; $\alpha = 0.01$), so that the heavier animals were more frequent in bone assemblages, even more if their population size is relatively larger than among other species with a similar body mass(Fig. 3). An example of this is that such an abundant species as the rabbit, with a population over 14,000 individuals in 1990, was represented only by four incomplete carcasses. In contrast, 31 cow carcasses were found from a population of more than 140 individuals.

However, there is no significant relationship in the group of large sized ungulates (50–400 kg). The species over 100 kg are no more frequent among the carcasses than those of between 50 and 100 kg, as was also seen in Amboseli National Park (Behrensmeyer and Boaz, 1980).

Foxes, wild boars and horses were more frequent among the carcasses than expected (Table 2), whereas red deer and cattle were

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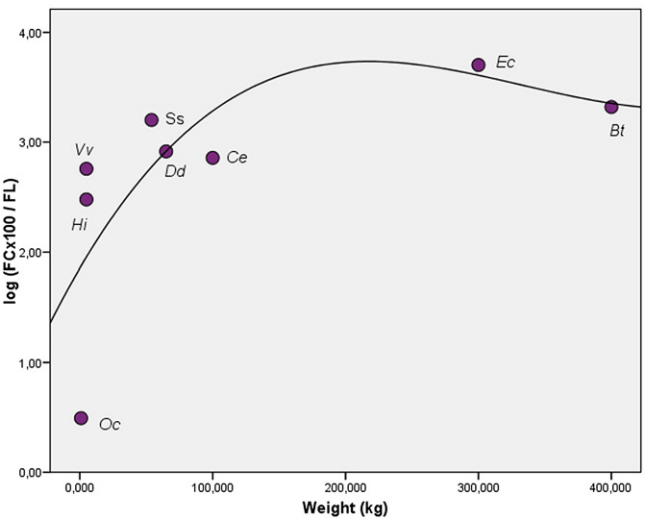

Fig. 3. Representation of the carcasses found in the samplings -FC- related to the population size -FL- and mass of each mammal species. The populations with a higher number of individuals and smaller body mass are underrepresented in the Doñana thanatocenosis.

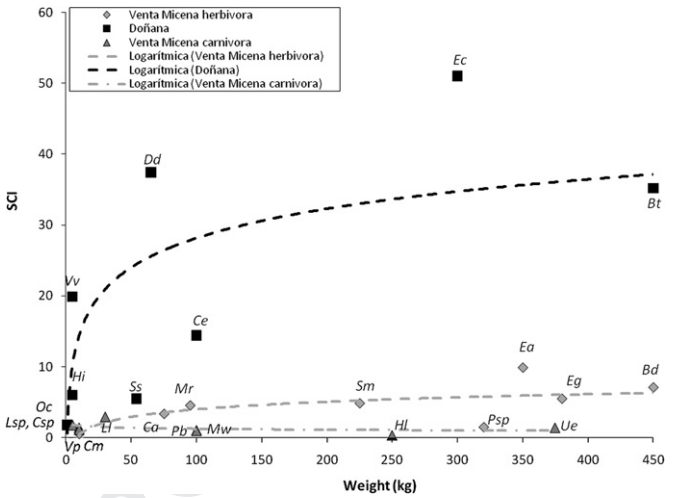

Fig. 4. Average preservation of the species -SCI- found in the thanathocenosis according to body mass (kg) in Doñana Biological Reserve and in the paleontological site of Venta Micena. Bt: *Bos taurus*; Ec: *Equus caballus*; Ce: *Cervus elaphus*; Dd: *Dama dama*; Ss: *Sus scrofa*; Hi: *Herpestes ichneumon*; Vv: *Vulpes vulpes*; Oc: *Oryctolagus cuniculus*; Bd: Bovini cf. *Dmanisibos*; Eg: *Eucladoceros giulii*; Ue: *Ursus etruscus*; Ea: *Equus altidens*; Psp: *Praeovibos* sp.; Hl: *Homotherium latidens*; Sm: *Soergelia minor*; Mw: *Megantherion whitei*; Mr: *Methacervocerus rhenanus*; Pb: *Pachycrocuta brevirostris*; Ca: *Capra alba*; Ll: *Lycaon lycanoides*; Cm: *Canis mosbachensis*; Vp: *Vulpes praeglacialis*; Csp: *Caprinii* sp.; Lsp: *Lynx* sp.

less frequent than expected, taking into account the population size and the body mass of these species.

In principle, two factors are involved in the representation of ungulate populations in the bone assemblages: body mass and population size. However, a third factor distinguishes the Doñana's thanatocenosis and Amboseli: the time span the bodies remain on the ground at a given ecosystem, which in turn involves differences in the state of preservation of the bodies. The Amboseli thanatocenosis was composed of recent carcasses, whereas in Doñana bone assemblages were sampled in different states of decay because the animals had died at different times. The average state of destruction of the carcasses of each species was measured by the percentage of preserved bones of the Skeletal Conservation Index (SCI) in the thanatocenosis of the two ecosystems with the greatest richness of species and abundance of individuals: *Monte* and *Vera*. The number of carcasses found in *Monte* and *Vera* was 107 (71.3% of the total) with a body mass over 1 kg. The SCI was in general much higher among the individuals with a larger body mass ($p = 0.045$; Rho = 0.719; g.l. = 7; $\alpha = 0.05$). However, analyzing the results for each species, two groups were noted: foxes, fallow deer and horses have a higher preservation percentage and rabbits, the Egyptian mongoose, wild boars and cattle have a smaller SCI (see SCI in Table 3). In this latter group, two species with a body mass of over 100 kg are underrepresented (Fig. 4), in contrast with the findings of Behrensmeyer and Boaz (1980) in the thanatocenosis of Amboseli National Park. This result is influenced by the time that the carcasses remained on the ground after death. Some of these carcasses were located soon after death by scavengers, and they had still not been affected by the full intensity of scavenging activity.

On a few occasions, the bodies of young carcasses were found on the ground in Doñana; 13 out of a total of 141 mammals. Nearly all of these (12 bodies) were ungulates under two years of age.

In the cork-oak woods in *Vera* and *Monte*, the only remains of young animals were of red deer, fallow deer, and wild boars. The relationship found between the number of juvenile and adult carcasses was 1:7 for red deer, 1:16 for fallow deer, and 2:17 for wild boars. The number of young carcasses was less than 15% of the total number of carcasses, in the case of these three species.

The individuals' age is a more significant factor than the body mass in the group of ungulates. One of the monitored cow carcasses preserved 45.3% of its bones after 16 months, whereas this cow's offspring, which was unborn, still preserved 6% of the skeleton. Even two individuals with the same body mass and different maturity (an adult deer and a calf) have different degrees of preservation. A calf (about 100 kg) preserved 24.5% of its bones after five months, whereas the red deer preserved 38.1% of its skeleton. The resistance of the bone tissue is perhaps the factor that determines greater scavenging activity on the young individuals.

Table 3
Sampling of *Vera* (ecotone) and *Monte* (scrublands) found 107 carcasses in various states of preservation. The skeletons of cows and horses are the best preserved. NB is the number of bones; MNI is the minimal number of individuals; NBS is the total number of bones of the skeleton and SCI is the Skeleton Conservation Index.

Species	Mass (kg)	NB	MNI	NBS	SCI
Bostaurus -Bt-	400	1.413	20	4.020	35.20
Equus caballus -Ec-	300	810	8	1.592	51.00
Cervus elaphus -Ce-	100	562	19	3.895	14.40
Dama dama -Dd-	65	2.375	31	6.355	37.40
Sus scrofa -Ss-	54	283	19	5.111	5.50
Vulpes vulpes -Vv-	5	280	5	1.405	19.90
Herpestes ichneumon -Hi-	5	17	1	281	6.00
Oryctolagus cuniculus -Oc-	1	20	4	1.088	1.80
TOTAL	–	5.760	107	23.747	24.30

4.2. An example of the scavenging activity according to corporal mass of animals

Although in Doñana the total number of deaths among the located species is not known, the first results on the dynamics of two populations in the study, rabbits and cattle, are available. Villafuerte (1994) monitored the survival of 310 young rabbits born in one year. While the young rabbits are inside the warrens, the survival rate is 78%, and once they leave this rate drops to 27% among individuals between one and three months old. The survival rate varied because when they remain in the rabbit holes they rarely experience the pressure of three reptile species (*Malpolonmon spesulanus*, *Natrix natrix* and *Lacerta lepida*). However, outside, they are also attacked by birds of prey (*Milvus milvus*,

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Milvus migrans, *Buteo buteo*, *Aquila adalberti*) and carnivorous mammals (*Vulpes vulpes*, *Herpestes ichneumon*, *Meles meles*). In both stages, inside and outside the rabbit hole, the rabbits suffer the occasional pressure of badgers and wild boars. After monitoring them for eight months, the researchers only succeeded in locating 19 individuals by radio-tracking; the survival rate was 6.13%. Such a high death rate should produce a large number of carcasses, mostly of young individuals. However, during the two years' sampling, only four adult carcasses were located in the entrance of a warren, after their fellow rabbits had cleaned it out in order to occupy it again.

Perhaps in the case of the large sized mammals it is easier to estimate the effect of scavenging because the time of destruction of the body is greater. Adult cattle are the heaviest animals in Doñana, over 400 kg, and in principle no predators or scavengers are capable of making their carcasses disappear completely. Therefore, it was expected that the total number of carcasses located would correspond to the total number of deaths that had occurred during the time of sampling, in different states of preservation. Lazo (1992) documented 160 calves born in three years from a stable population of 140 cows, and in those three years found 27 carcasses. Of these carcasses, 10 were adults and 17 were infants. If the population did not rise above the 140 individuals, then only 10 calves survived. In addition, 45 calves were withdrawn by cattle ranchers (28.13% of those that had been born). These values indicate a total of 72 calves, and therefore 88of them could not be located. It is possible that these young carcasses had been scavenged completely, or nearly completely.

In conclusion, populations of species with greater body mass, even with a smaller number of dead individuals, provide more carcasses for thanatocenosis due mainly to their corporal mass. Body mass is a factor which favours the skeleton preservation of the heaviest animals on the ground.

4.3. A place to live, a place to die

During the sampling in Doñana, it was observed that when an animal is dying it seeks shelter, it needs to hide from predators, it requires water and food, and if possible, some type of alarm for the presence of predators, such as a bird colony. All this can be found in Doñana in some biotopes, but above all in a very rich ecosystem in living species, *Vera*, the ecotone between *Monte* and *Marismas*. The distribution of carcasses in Doñana was studied in the 12 biotopes within the four ecosystems (Table 1).

Vera contained 16 carcasses/km^2, consisting of eight species: five ungulates, two carnivores and a lagomorph (the same faunistic richness than the mammal thanatocenosis in the DBR). *Monte* recorded 5.5 carcasses/km^2, belonging to five ungulate species and a lagomorph. The values were smaller in the salt-marsh, as three ungulates were found with a density of 8.3 carcasses/km^2. Finally, in the dunes two ungulate species were recorded, with a density of 16.7 carcasses/km^2. Therefore, *Vera* was the ecosystem with the greatest richness of species and one of the highest densities of carcasses.

Some of the biotopes had wider species richness than the ecosystems themselves (Table 1). The richest areas in species were woodlands, peri-lagoon areas and pastures. Biotopes with plant cover, presence of water and the highest faunal richness had the highest carcass density and dead species. In the pine-wood, the only carcass recorded was a of a fox, whereas in the cork-oak woods both in *Monte* and *Vera* a carcass was found under each tree; among the 10 cork-oaks in the *Monte* there were 12 individuals, and under the 51 trees in the *Vera*, 47 carcasses were recorded.

The two biotopes of *Vera* that were studied, the pasture (an open area) and the cork-oak wood (an enclosed area), contained different densities of carcasses, although the faunal richness in the community was the same. The cork-oak wood, an area of 1.02 km^2, contained the same number of carcasses as the pasture, which is five times larger in area. So, it was deduced that in *Vera*, the covered areas (cork-oak wood) are the preferred habitats to die.

In Doñana, most of the carcasses were found near water-courses and under the cork-oak woods with an undergrowth of bracken (a few metres away from the pastures where they lived). In Amboseli, the biotopes with the largest percentage of preserved carcasses were open places near water-sources, the salt-marshes (Behrensmeyer and Boaz, 1980). In Amboseli the highest density of carcasses could be explained by the behaviour of carnivores (which hunt in open areas), in Doñana the distribution reflects the behaviour of the sick animals (which seek refuge).

4.4. Estimating the age of a thanatocenosis: fossil potential

The death rate for each species will provide the number of bodies produced per year, a necessary variable to analyze the representation of the community in its thanatocenosis (fossil potential, according to Behrensmeyer and Boaz, 1980). Cows were the only case in Doñana in which the turnover rate and death rate were known. Lazo (1992) estimated that the cattle population in Doñana (from 1987 to 1989) was140 individuals of more than one year of age. He also calculated that the death rate for adults was 8.33%. According to these values, the expected number of bodies should be about 11every three years. According to this data, the 31 carcasses found in Doñana's thanatocenosis would have occurred in nearly nine years. Nevertheless, as the death rate of each species is unknown (as is the case of the oryctocenosis), the date of death could only be estimated from the relationship between the preservation status of a body and the time since its death.

The time taken between the death of a vertebrate and the disappearance of the carcass from the land surface depends mainly on the body mass (and on the presence of bone-scavengers in current ecosystems). Other factors accelerate or decelerate the post-mortem processes, such as the population, ethology, the individual's age, the biotope in which it dies (the type of vegetation obstructs (or not) the location of carcasses by scavenging birds), and occasional (mud flows, illnesses) or recurrent events (the rut). A total of 24 carcasses were monitored during more than two years (7 cows, 3 horses, 5 red deer, 5 fallow deer, 3 wild boars and 1 fox), of which 17 were used to describe the general pattern of the preservation of mammal carcasses over 5 kg in mass. This can be summarised in three phases:

4.4.1. Phase I. Loss of soft mass of body

The soft tissues are consumed by invertebrates and vertebrates, and most of the skeleton is preserved. Álvarez et al. (1976) observed that only vultures break ribs and consume some phalanges in red deer carcasses. The average time of this phase is less than two months.

4.4.2. Phase II. Maximum velocities of skeleton disarticulation, bone dispersion and bone loss

Three models of carcasses destruction are defined, depending on the values of these variables and SCI (Fig. 5), and time varies depending on the mass of the animals:

a) Type I. Animals with body mass of over 200 kg: cattle and horses. The SCI at the end of Phase II is larger than 48, the disarticulation rate *d* fluctuates between 10 and 15 (percentage of bones disarticulated each month), the dispersion rate *s* is between 19 and 21 (increase of the dispersion area of bones per month) and the bone loss rate *p* is between 7 and 10

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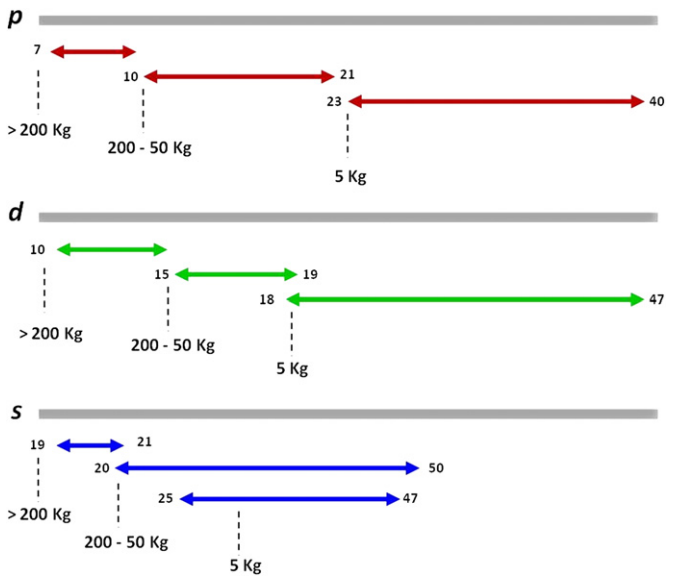

Fig. 5. Values of the variables measured in the monitoring of the post-mortem processes of 17 carcasses. *p* is the bone loss rate, *s* is the bone dispersion rate and *d* is the bone disarticulation rate of the monitored carcasses in Doñana Biological Reserve according to body mass (kg).

(percentage of bone lost per month). The average time of Phase II in these animals is from five to eight months. The disarticulation and the loss of bones in the heavier carcasses depend on the arrival of the large scavenging birds.

b) Type II. Animals between 50 and 200 kg in mass: red deer, fallow deer and wild boars. The SCI oscillates between 42 and 21, *d* is between 15 and 19, *s* is between 20 and 50 and the bone loss rate *p* is between 10 and 21. In carcasses of less than 100 kg the disarticulation of the skeleton did not depend only on the vultures, and the main scavenger was the wild boar. The average time of Phase II in these animals is about four months.

c) Type III. The monitored carcasses were of an adult fox and a new-born fallow deer, both about 5 kg in mass, and wild boars were again the main bone-scavengers. The SCI did not go above 17, *d* oscillated between 18 for the fox and 47 for the young fallow deer, the dispersion *s* varied from 25 to 47 and the bone loss rate *p* is between 23 and 40. The carcasses of this type usually disappear from the ground within a year. The average time of Phase II in these animals is less than four months.

4.4.3. *Phase III. Slowing the destruction of the skeleton*

This is the period of time in which the bone loss rate in the carcasses becomes minimal. The total destruction of the carcasses of more than 50 kg can take years. In March 1989, two red deer carcasses which had died six years ago (oral communication, wardens) were located. One preserved 7.3% of the skeleton and the other 5.4%. Of a third red deer which had died in 1986, 4.5% of the total skeleton was found; a fallow deer which had died in November 1987 had 15.6% of its bones; and a wild boar with the same date of death preserved 10.8% of its skeleton (Bernáldez Sánchez, 2009). Six years after the date of death, an ungulate preserved less than 10% of its skeleton. Behrensmeyer and Boaz (1980) mentioned that 5% of the bones of ungulate carcasses usually become buried. A similar percentage is found in Holocene archaeological sites (Bernáldez Sánchez, 2002b; Bernáldez Sánchez and Bernáldez Sánchez, 2002, 2003a, 2003b; BernáldezSánchezet al., 2010).

According to all these results, the age of the thanatocenosis(or Phase of destruction) composed of 107 carcasses located in *Monte* and *Vera* from the average SCI of the carcasses of each species (Table 3) was estimated:

- The average SCI from the 20 adult cows that were located was 35.5%, so it was deduced that this bone assemblage was in the beginning of Phase III.
- The eight horses found in sampling scrubland and *Vera* had an average SCI of 50.9%, and this percentage shows that this bone accumulation was between Phases I and II.
- The mean for the skeletal conservation obtained for the 19 red deer was 14.4%, which implies that this association was in Phase III.
- The average SCI from 31 fallow deer was 37.4%, so it was deduced that this bone assemblage was in Phase II.
- The 19 wild boars recorded in *Monte* and *Vera* had an average SCI of 5.5%, and this carcass association was in Phase III.
- The mean for the skeletal conservation obtained for the five foxes was 19.9%, so it was deduced that this bone assemblage was in Phase II.

To sum up, the thanatocenosis of the terrestrial mammals sampled in Doñana from February 1989 to April 1990 consisted mainly of individuals which had died in the previous 29 months, except for the few cows and red deer mentioned that exceeded this time.

Another consequence of these results is that the largest animals are not always better preserved when studying a complete thanatocenosis; in contrast with the results obtained in the monitoring of 17 carcasses in Doñana. The relationship between the average SCI and the body mass of each species (Fig. 4) indicated that foxes, fallow deer and horses were better preserved than expected, in contrast with red deer, wild boars and cows. This is explained by the different phases of the carcasses found.

5. Biostratinomy of Doñana applied to the palaeontological site at Venta Micena

The starting point of this paper was the discussion in Martínez-Navarro (1991) about the possible similarities in the geological and palaeobiological characteristics of Venta Micena and Doñana Natural Park (Huelva), a Mediterranean-type arid zone. The site at Venta Micena (Orce, Granada) is situated in the eastern sector of the Guadix-Baza lacustrine basin. According to Martínez-Navarro (1991), the biostratigraphic and systematic analyses of the large mammals documented in the lacustrine sediments date the site in the Lower Pleistocene (1.5 ± 0.1 Ma). Arribas and Palmqvist (1998, 1999) and Palmqvist et al. (1996) concluded that the accumulation of remains is due to the activity of the giant hyenas that lived at that time. The biostratinomic characteristics of this assemblage gives a biased picture of the community, except in the case of species larger than 50 kg in mass, which are all present in the thanatocenosis. The best-represented species are those with individuals that have died recently, with the largest populations, and with the greatest body mass.

Of this bone assemblage 107 carcasses from *Monte* and *Vera* were found in different states of conservation (SCI), varying between 1.8% of the rabbit skeletons and 50.9% of the horse bones (Table 3). They were almost all in Phase II of the dynamics of scavenging activity, and they were animals that had died within the previous 29 months, apart from the exceptions that were described. The accumulation of recent bones, and to a lesser extent, of individuals, was significantly correlated with the body mass of the carcasses ($p = 0.014$, Rho = 0.817, g.l. = 7 for the number of specimens; $p = 0.054$; Rho = 0.609, g.l. = 7 for the minimal number of individuals (Fig. 6). The largest accumulations corresponded to the

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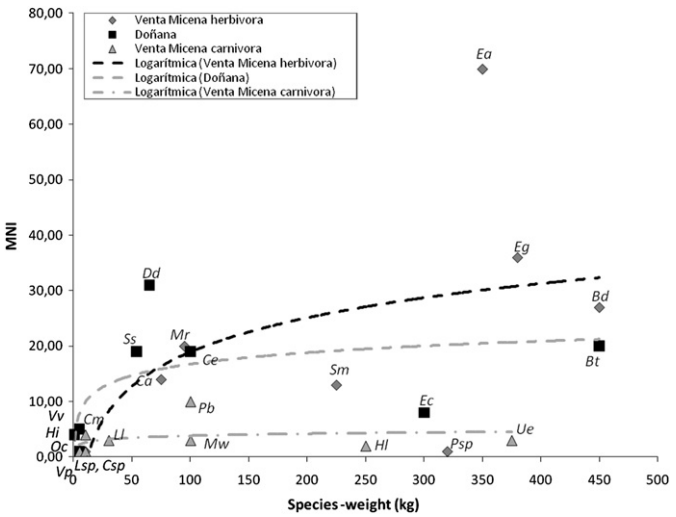

Fig. 6. Minimal number of individuals (carcasses) found in the thanatocenosis -MNI- according to body mass (kg) in Doñana Biological Reserve and in the paleontological site of Venta Micena. Bt: *Bost aurus*; Ec: *Equus caballus*; Ce: *Cervus elaphus*; Dd: *Dama dama*; Ss: *Sus scrofa*; Hi: *Herpestes ichneumon*; Vv: *Vulpes vulpes*; Oc: *Oryctolagus cuniculus*; Bd: Bovini cf. *Dmanisibos*; Eg: *Eucladoceros giulii*; Ue: *Ursus etruscus*; Ea: *Equus altidens*; Psp: *Praeovibos* sp.; Hl: *Homotherium latidens*; Sm: *Soergelia minor*; Mw: *Megantherеon whitei*; Mr: *Methacervocerus rhenanus*; Pb: *Pachycrocuta brevirostris*; Ca: *Capra alba*; Ll: *Lycaon lycanoides*; Cm: *Canis mosbachensis*; Vp: *Vulpes praeglacialis*; Csp: *Caprinii* sp.; Lsp: *Lynx* sp.

heaviest species and in addition, their skeletons were also the best preserved ($p = 0.045$, Rho = 0.719, g.l. = 7 (Fig. 4).

The mammal thanatocenosis in Doñana of 5–400 kg in body mass (without rabbits) shows the previous trend (Fig. 3): the heaviest species are not necessarily the best preserved and nor are they represented by a larger number of individuals, although the number of remains is larger ($p = 0.041$, Rho = 0.708, g.l. = 7). Finally, considering the dynamics of the preservation of species between 50 and 400 kg in mass, there is no significant correlation between the accumulation (of bones or bodies) and their SCI, with regards to their body mass. In this case, the species with the largest populations are usually represented by a proportionally larger number of carcasses.

The main difference between the thanatocenosis in Doñana and the taphocenosisat Venta Micena lies in the number of mammal species recorded (eight in Doñana and 28 species in the paleontological site) and in the range of body mass, which reaches 6,000 kg at Venta Micena. These characteristics could indicate different dynamics of scavenging activity, but some patterns of the accumulation of remains in both associations are similar. The wide range in body mass should open the possibility of a larger range of predator and scavenger species, as can be seen in the species list (Martínez-Navarro, 1991). Whereas in Doñana the body mass discriminates between the species of two trophic groups, the herbivorous mammals of over 50 kg in mass and the carnivores of less than 15 kg in mass, at Venta Micena large herbivores and carnivores in the same range of body mass co-existed. This will affect the dynamics of carcass conservation.

5.1. Venta Micena: the Doñana of the Pleistocene?

The taphonomic analysis of the Venta Micena oryctocenosis is based on the biostratinomic study in Doñana. The fossil assemblage for species between 5 and 6,000 kg in mass consists of 2796 identified osseous remains (and 3010 teeth that were not included in the calculation of the SCI) belonging to 225 individuals (MNI in Table 4). The studied patterns at Venta Micena for animals with

Table 4
List of species at paleontological site of Venta Micena (Orce. Granada) (Martínez-Navarro, 1991; Palmqvist and Arribas, 2001; personal communication). This table presents the values of the accumulation of specimens (NISP) and individuals (MNI). and the skeleton preservation index (SCI) in the fossil assemblage. The species with more than 3% in SCI are marked in grey; all are ungulates more than 75 kg.

Species	Mass (kg)	NISP	MNI	SCI	Juv/adult index
Vulpes praeglacialis	5	5	1	1.79	0
Lynx sp.	10	4	1	1.43	0
Canis mosbachensis	10	13	4	1.16	0
Caprini gen. et sp. *indet.*	10	1	1	0.49	0
Lycaon lycaonoides	30	25	3	2.98	0
Capra alba	75	96	14	3.34	0.17
Methacervocerus rhenanus	95	186	20	4.54	0.18
Megantherеon whitei	100	9	3	1.07	0
Pachycrocuta brevirostris	100	28	10	1.00	0.67
Soergelia minor	225	129	13	4.84	0.30
Homotherium latidens	250	2	2	0.36	0
Praeovibos sp.	320	3	1	1.46	0
Equus altidens	350	1.379	70	9.90	0.84
Ursus etruscus	375	12	3	1.43	0.50
Eucladoceros giulii	380	405	36	5.49	0.71
Bovini cf. *Dmanisibos*	450	393	27	7.10	1.45
Stephanorhinus etruscus	1500	35	6	2.17	0.50
Hippopotamus antiquus	3000	39	5	2.90	1.50
Mammuthus meridionalis	6000	32	5	2.38	4.00

corporal mass between 5 and 6000 kg are similar to those observed in Doñana (5–400 kg): the species with the largest body mass significantly contribute toa larger accumulation of specimens ($p = 0.044$, Rho = 0.462, g.l. = 18) and the larger species are not necessarily represented by a high SCI or by a high MNI.

At Venta Micena, the SCI oscillates between 0.36% of *Homotherium latidens* (a carnivore about 250 kg) and the 9.9% of *Equus altidens* (a herbivore about 350 kg).In general, these values are lower than those obtained in Doñana (between 1.8% for rabbits and 50.9% for horses(Fig. 4). As in Doñana (extended study in Sierra Norte de Sevilla Natural Park; Bernáldez Sánchez et al., 2008), these low preservation indexes would correspond to Phase III, and a SCI lower than 10% for animals weighing over 200 kg would correspond to animals that had died at least 29 months previously. In Phase III the rates of skeleton disarticulation, bone loss and bone dispersion are much reduced (in Doñana, a red deer still preserved 7.3% of the carcass after six years since its death, and a cow preserved 10% of the skeleton after ten years since its death). According to the values obtained for SCI at Venta Micena, if the hyenas acted in the same way as modern hyenas (Pokines and Kerbis-Peterhans, 2007), it is possible that the times calculated for carcasses to remain on the land surface at Venta Micena are longer than what occurred among the community in Doñana.

For the skeleton preservation values (SCI) for the species at Venta Micena (Table 4), some herbivores (5 species with 10–6000 kg) and all the carnivores (5–250 kg) show SCI no greater than 3%. The carnivore bone assemblage (without including the omnivorous *Ursus etruscus*), displays a pattern which is unexpected from the scavenging activity that had been described in Doñana. Among the group with a SCI less than 3%, the smaller carnivore species at Venta Micena have a higher SCI ($p = 0.046$, Rho = −0.764; g.l. = 6) and, in contrast, the largest herbivores are better represented ($p = 0.037$, Rho = 0.9, g.l. = 4). The group with a SCI higher than 3% consists of six herbivore species between 75 and 450 kg in mass (Table 4) where in general the heaviest are the best preserved ($p = 0.042$, Rho = 0.829, g.l. = 5).

In Doñana, the main preservation factors for a scavenged carcass are the body mass, the age and the population size. The canids (10 kg) at Venta Micena are significantly better preserved than the sabre-tooth tigers (250 kg) ($p = 0.046$, Rho = −0.764; g.l. = 6). It is

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possible that the scavenger activity will decrease if the number of carcasses is high in a short time. The monitoring of the post-mortem scavenging activity on the carcasses of cows 3 and 4 (Fig. 7) in Doñana might explain this situation (Bernáldez Sánchez, 2009). Both died at the same time and were left in the meadow in the *Marisma* a few metres apart. After seven months they still preserved 88% of the total number of bones of both skeletons. Meanwhile, in the same length of time, cow 1, which had died the year before in the same pasture, preserved 59.2% of the total skeleton and cow 2, in a nearby pasture, preserved 47.3% of its bones on the ground surface. These values were not caused by a better bone preservation of cows 3 and 4, but of one of them (see Fig. 7). The large scavengers, vultures and wild boars, had acted on one individual, whereas the other went several months without being disarticulated. It is possible that the mass of carrion provided by one cow was sufficient for the number of scavengers that fed from it. In other words, a stable population of scavengers have a certain "thanatomass" of consumption. If this increases in a short space of time (hours or a few days), the additional carcasses are scavenged less intensively. In fact it is striking that until they finish with one carcass, the scavengers do not start on the next one, or at least they do not scavenge it with the same intensity. In this way, the better bone preservation of the horses (SCI 9.9%) at Venta Micena would be the result of a reduced scavenging activity, due to a large concentration of deaths at a short period of time.

In general, this low percentage of bones preserved at Venta Micena, less than 10% of the skeleton even in the best cases, seems to suggest that the carcasses were exposed long enough for the scavenging activity to be intense. The burial of the osseous remains might have taken place, as in Doñana, either by the growth of vegetation (Fig. 8) or by the mud from small water-courses. These sources of underground water resemble the basins found at Venta Micena (Martínez-Navarro, 1991).

5.2. Dominant species and sexes

At Venta Micena, the horses display both the highest SCI (9.9%) and the greatest abundance (70 individuals) in the fossil assemblage. In Doñana, the carcasses of horse presented the best preservation (SCI 50.9%) and a small number of individuals (Table 3). Nevertheless, this species was over-represented with regard to size population (Fig. 3). This over-representation was due to the recent death of the individuals (Phases I and II), in contrast, the horses at Venta Micena were exposed for a long time to the scavenger activity before being buried (Phase III). In consequence, the high number of horses at Venta Micena could be due to a great concentration of bodies in correspondence with a great size population or a short time of death.

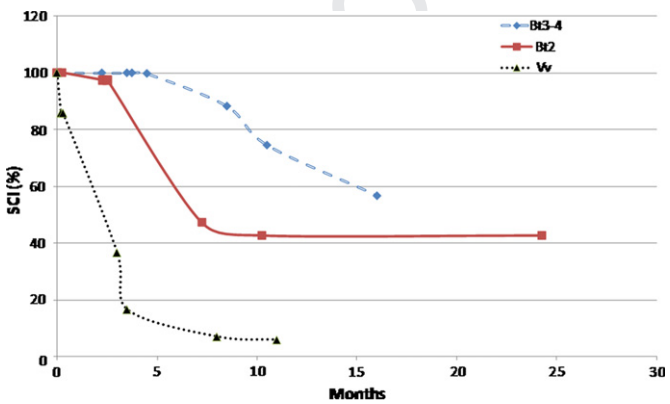

Fig. 7. Differences between the dynamics of scavenger activity in carcasses of different mass (cows *vs.* a fox -*Vulpes vulpes*-). This activity is lower w[illegible]wo carcasses are close together (*Bostaurus*3-4) (Doñana Biological Reserve, 1990).

Fig. 8. Bones that were not scavenged and w[illegible]ried by the vegetation in the ecosystem *Vera* (Doñana Biological Reserve, 199[illegible]o by E. Bernáldez Sánchez.

Another aspect worthy of attention is the imbalance in the sex ratio of *Eucladoceros giulli*(Martínez-Navarro, 1991), where almost all the individuals are male. At the present time, in Doñana, the death rate of male fallow deer increases after the rut, in October and November (Braza et al., 1984). Most of the carcasses are found in the cork-oak wood in *Vera*, although the usual habitat of this species is marshes (Bernáldez Sánchez, 2009).

5.3. Juveniles: large and abundant

During the sampling in Doñana between November and December 1989, found beneath the cork-oaks in *Vera* were the carcasses of juveniles and adults belonging to three species in these proportions: one juvenile and seven adult red deer (over 75 kg in mass); one juvenile and 16 adult fallow deer (over 65 kg in mass) and two juvenile and 17 adult wild boars (over 54 kg in mass). At Venta Micena, these herbivores were found in similar proportions: *Soergelia minor* with three juveniles and 10 adults (over 225 kg in mass); *Methacervocerus rhenanus*, with three juveniles and 17 adults (95 kg) and *Capra alba* with two juveniles and 12 adults (75 kg). There does not seem to be any great differences between the bone and the fossil assemblages in terms of the proportions of juvenile and adult individuals of the selected species. Considering the relationship between the proportion of juveniles and adults at Venta Micena and the body mass, the heaviest species had a larger proportion of juvenile individuals in comparison with the number of adults ($p = 0.001$, Rho = 0.866, g.l. = 10 and n.s. = 0.01).

The values for juvenile/adult ratio estimated in Doñana were: 1.7 for cows, 0.14 for red deer, 0.06 for fallow deer and 0.12 for wild boars. The heaviest species preserve more juveniles, except among the wild boars. Their higher representation, despite being the

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Fig. 9. Photograph from the film "Ecology of the Death", presented with various scientific awards. This film shows the scavenger activity of the wild boars in the Mediterranean ecosystems. Photo by A. Menor.

lightest of the ungulates, is compensated by the highest birth rate which increases the probability of representation of young dead.

The 19 species analyzed at Venta Micena(in the last paleontological excavation some new taxa have been found) display a significant correlation between the juvenile/adult ratio and the body mass ($p = 0$, Rho $= 0.804$, g.l. $= 18$, $\alpha = 0.01$). Nevertheless, in the case of herbivores between 75 and 450 kg in mass, there is a correlation between the juvenile/adult ratio and the NMI ($p = 0.036$, Rho $= 0.786$, g.l. $= 6$, $\alpha = 0.05$). This correlation is not found among the carnivores and the mega-herbivores.

5.4. Community, thanatocenosis and taphocoenosis

Finally, an attempt was made to calculate the correlations between the thanatocenosis in Doñana, the taphocoenosis at Venta Micena and the biocoenosis in Doñana. Simpson's dominance index (Simpson, 1949) for the Doñana community of 50–400 kg in mass is 0.28, for the sampled thanatocenosis the same index is 0.22, and the oryctocoenosis at Venta Micena gives a very similar value, 0.23. The thanatocenosis in *Vera* (DBR) and the taphocoenosis at Venta Micena have similar values. This would be understandable if the ancient community at Venta Micena and the current community in Doñana were similar in faunistic composition, but they are not. If Doñana, with no hyenas or large predators, displays similar biostratinomic characteristics to an oryctocoenosis with a higher species richness, it is because the bone scavenging activity of the hyenas at Venta Micena has its equivalent in the activity of the suids (Fig. 9) in Doñana.

Acknowledgements

I would like to thank Dr.Martínez-Navarro for his helpful review of this paper and Esteban García-Viñasand Aurora Ocañafor his assistance.

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