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CURRENT TOPICS ON TAPHONOMY AND FOSSILIZATION

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Biostratinomy of terrestrial macromammals in Doñana National Park (Spain)

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INTRODUCTION

There is no scientific guarantee that vertebrate remains preserved in archaeological and palaeontological sites are a representative sample of the palaeocommunity they belonged to, or that they formed a part of the preferences of man consumption since they are mainly waste deposits. We do not know the qualitative and quantitative consequences of pre-depositional processes of trophic activity of human population and of any other carnivore and scavenger that could have affected them. As a consequence of this, we performed a biostratinomic study of the carcasses assemblage scattered throughout the Doñana Biological Reserve in order to know if there is a preservation general dynamics, with general patterns that can be applied to the taphonomic study of archaeological sites.

The palaeobiological interpretations given in archaeozoological studies lack the taphonomic and biostratinomic reference information that guarantees the reliability of such interpretations. For that reason I have studied the formation of a natural bone deposit as the first goal of a wide work developed during more than twelve years, oriented to determine the general trends in the formation of superficial and buried bone assemblages, explaining one of the less studied trophic manifestations of man: garbage dumping sites. So far, a general methodology of study has been designed, which allows to compare the pre-depositional characteristics of any anthropic or natural thanathocoenosis and taphocoenosis.

This methodology has been inferred from the biostratinomic study of macromammals inhabiting the Doñana Biological Reserve (DBR) (Huelva, SW Spain). In this study I observed the trends in selected variables related to the following two concepts: accumulation per surface unit and individual preservation. I have used these two concepts to characterise bone deposits and to quantify the loss or gain of biological information from them. A bone deposit is considered as a present entity formed in the past, with no warrant that it would be preserved.

MATERIAL AND METHODS

The Doñana Biological Reserve has four well-differentiated ecosystems: scrublands (the so-called 'Monte'), sand dunes, marshlands, and the so-called 'Vera' (Amat, 1979; Delibes, 1980; Alés, 1987). This last ecosystem is in fact the ecotone between marshlands and scrublands, where the highest faunal and floral richness is found (Soriguer, 1981). There are 125 bird species, 28 mammals, 17 reptiles, 9 amphibians, and 8 fish species (Delibes, 1992; Hernando, 1978), represented in the thanathocoenosis sampled between 1989 and 1991 as follows:

1.- The terrestrial vertebrate community from the Doñana Biological Reserve is not represented in the studied thanathocoenosis between 1989 and 1991. Among 280 identified species only 13 vertebrate species remains have been found, that is 5%.

2.- The mammal community is best represented by species with a body weight equal or above 1 kg because, while the birds and reptiles are represented by 1% and 9% respectively, the mammals form the 29% of living species. In this mammal group, six ungulate species are present, all with more than 50 kg of body weight; two carnivores among the nine species that exist at the present time, and two lagomorphs (the European rabbit and the Mediterranean hare, with less than 3 kg of body weight). The application of direct observation methodology for sampling did not provide any bone remains of small mammals.

3.- The Doñana thanathocoenosis studied between 1989 and 1991 show formation rules similar to those observed by Behrensmeyer & Boaz (1980) in Amboseli National Park (Kenya). The observed differences between both reserves identify the more or less intense activity of scavengers and carnivores that are a part of the community either permanently or seasonally (scavenging birds). In both ecosystems, Doñana and Amboseli, carcasses accumulation follows similar patterns:

3.1. All the species whose individuals have a body weight above 50 kg are present in the thanathocoenosis.

3.2. As individual body weight increases, the carcass frequency on the ecosystem surface increases as well. This general trend has been observed in Doñana and Kenya but with some limitations: in Doñana it is significant only in mammals with a body weight between 1 kg (rabbit) and less than 1000 kg (camel) (Pearson correlation test Log (FT/FVx10), r2 = 0.83, p = 0.0057, g.l.= 8; being FT carcass frequency and FV frequency of living individuals), ungulates with weights above 50 kg do not show this dependence. This situation can also be deduced from the similarity in the carcass number of three species with different population sizes. Thus, I have found 31 cows, 36 deer and 31 wild boars carcasses but the population sizes are 170 cows, 500 deer and 223 wild boars. In Amboseli, the later trend is found in ungulates with body weight between 25 kg (impala) and 2500 kg (elephant).

3.3 Some seasonal and occasional behavioural events, such as ungulate rutting ('ronca' and 'berrea' in Autumn deer and fallow deer), epizootics (plague during 1988 in wild boars) and climatic events (flooding, sand dunes movements, drought), cause a higher mortality rate in mammal populations. This fact is registered in carcass frequency (Braza, pers. com.) and bone remains. If there is no scavenger population increase implying a rise in scavenger activity, the carcass frequency in those high mortality periods will be obvious in the thanathocoenosis. E.g. in the 'Vera' we find 59 carcasses (45.8% of the total amount), 27 in November 1988 and 1989; 21 of them were still complete, that is, they were recently dead.

3.4. Neither the mammal community composition nor the age structure are represented in the bone assemblage. The first one has been already explained and the second characteristic is observable in the low frequency of observed youngs of any size. The higher observed frequency of located young carcasses is in ungulates, between October and November, they disappear from the surface in a few months, and are found in these proportions of juveniles-adults: deer 1-7, fallow deer 1-16, and wild boars 2-17.

3.5. The carcasses distribution in different biotopes is an indicator of species habitat preference and of the abundance of carnivores and scavengers in the area. The carcass density was 10.8 vertebrate carcasses/km^2, with body weights ranging from 80 g to more than 400 kg (n = 150 individuals); in this sample, 10.2 corresponds to mammals, 95% of them being ungulates: 9.5 carcasses/km^2. The observed density in the Doñana Biological Reserve (76 km2) was 2 carcasses/km^2 and 1.73 carcasses/km^2 for ungulates with a body weight similar or higher than 50 kg.

In Amboseli, the estimated carcass density for the 1188 registered bodies in a 8.75 km^2 sampling area is 135.8 individuals/km^2. It is, however, curious that this big difference with Doñana becomes almost insignificant when we make the comparison using the total surface of both parks. Then the carcass density in Amboseli is 1.98 individuals/km^2. Perhaps this difference between samples can be a reflect of a higher mortality or a better remains preservation in Amboseli with regard to Doñana or just a sampling effect. While in Amboseli 1.5% of total surface of the park was sampled, in Doñana 18% was sampled, almost 14 km^2.

Among the results obtained in Amboseli and Doñana, we have noted that most of ungulate carcasses are found under cork oaks of the 'Monte' and the

'Vera', surrounded by patches of ferns and blackberries that are more than 1 meter high. In Amboseli, the higher frequency of ungulate carcasses is found in the marshlands, an area with plants less than 50 cm high, practically an open land. From this fact, we infer that in Amboseli most carcasses are predation products (big carnivores hunting from gazelles to elephant calves choose open areas where herds are found). In Doñana, however, the main determining factor for remains distribution are sicknesses that make the animals look for refuge and water under these trees.

Besides this, I have confirmed that the aggregation index F= s2/x (a ratio between variance and mean) of the bodies contents of each biotope is higher than 1. This indicates that the probability of finding a carcass is higher where another one is found. Considering each species, we find that the highest body frequency of deer is in 'Monte', in the closest areas, which is coincident with habitat preference of this species. The same happens with the studied cows, fallow deer, wild boars, mongooses, foxes and rabbits. All them have their own death places, always of them in the 'Vera' biotopes.

3.6. As for the skeletal preservation, we have found 5760 bones of the expected 23747; they correspond to 107 mammal individuals, that is, we did not found 75% of the bones. Bone density per km^2 is 75.78 for the 76 km^2 of DBR, and 417.39 for the 13.8 km^2 sampled area, while in Amboseli 33.45 bones/ km^2 for the 600 km^2 of the basin, and 2.29 x 103 for the sampled area (8.75 km2) were registered. Even though the heaviest animals such as cows and horses possess a number of bones in their skeletons significantly lower than lighter species ($r = -0.84$; g.l. = 7; $p = 0.007$), the first ones have a higher number of bones preserved on the Doñana surface. The relationship between both variables, number of bones NB and body weight W is significant as expressed in the following equation ($r = 0.836$; g.l. = 7; $p = 0.009$)

$$\text{Log NHB} = 3.172 + 0.714 \text{ Log W}$$

Although the heaviest animals show a higher number of bones preserved on the surface, it was verified whether this amount justified a higher presence of them. The percentage of preserved bones per recorded individual, or Skeletal Conservation Index (SCIn) shows exactly this: the animals with a higher body weight are better preserved ($r = 0.773$; g.l. = 7; $p = 0.024$):

$$\text{Log SCIn} = 1.164 + 0.416 \text{ Log W}$$

3.7. The anatomical parts are differentially preserved. In the macromammal thanathocoenosis of Doñana the representation of bones from the trunk and limbs is similar to that of a complete body, where 83% of the skeleton bones would correspond to the trunk and limbs. It does not happen the same with the representation of bones from the head, where the observed percentage is higher than expected and its preservation is superior to that from other parts. This three anatomical parts have experimented a significant loss of bones (X2 = 13742; g.l. = 2; $p < 10$) due to a higher bone representation of the head (X2 = 6.99; g.l. = 2; $p = 0.015$) with regard to the expected one: 8% for the head, 40% for the trunk and 51.3% for the limbs. The observed percentages of representation have been 16.5% for the head, 40.6% for the trunk, and 42.8% for the limbs.

This is much easier to see using the SCIn. The observed carcasses conserve 46.1% of bones from the head, 24.6% from the trunk and 20.3% from the limbs. This means that the head is the better preserved anatomical part. This preservation has shown some differences among species. With exception of deer and rabbits, all the other species conserve more than 40% of the total of bones from the head, and less than 40% of the bones form the trunk and limbs.

THE FOSSIL POTENTIAL OF VERTEBRATES ASSEMBLAGE

Regarding the observed differences of bone preservation among different located bodies, we monitored 24 carcasses of macromammals during a period of two years with the following goal: to know the causes that determine the characteristics of the preserved bone assemblage on the surface of a natural ecosystem. The term 'fossil potential' of each species means the temporal variation of the percentage of preserved bones for each carcass. The results explain why the cow carcasses are better preserved than the rabbit ones even if cows have a population size of 170 individuals and the rabbits are more than 15000 specimens.

The destruction of those bodies since the animal death can be explained in three phases as a function of speed of bone loss (*p*), disarticulation of the different anatomical parts (*d*), and dispersion of the bones on the surface (*s*). Thus, I have observed that in the first phase, scavengers consume the soft parts of the carcass which does not experiment any loss of skeleton nor it is disarticulated. The second phase is characterised by a quick and positive increase of disarticulation, bone loss and dispersion rates, promoting the largest percentage of bone loss in the area. At the same time, the effect of the putrefaction acids is noticeable in the vegetation clearings surrounding the carcass. As I have checked, these areas present a higher acidity than the nearby ones. In the third phase, although all these three rates increase, the destruction of the carcass slows down.

Time and periodicity of the observed values in the carcass temporal preservation provide variants of the general tendency, considering the end of the positive increase in the Skeletal Conservation Index SCIn values at the end of the second phase:

Type I. Presented by animals with a body weight over 200 kg, body preservation state (ICEn) is over 48%, disarticulation rate fluctuates between 10% and 15%

(percentage of disarticulated bones per month), dispersion rate between 19% and 21% (monthly increase of the initial dispersion area), and bone loss oscillates between 7% and 19% (percentage of lost bones per month). More than 40% of the bones from skull, jaws, ribs, vertebrae and limb large bones are preserved. The start of scavenging is seasonal, depending on the vultures arrival to DBR at the beginning of Autumn.

Type II. It appears in animals from 200 kg to more than 50kg, the preservation state (SCIn) of carcasses oscillate between 42% and 21%, the disarticulation rate between 15% and 19%, the dispersion rate between 20% and 50% and the bone loss between 10% and 21%. More than 40% of the skull bones, jaws, vertebrae, and limb large bones are found on the surface, the breastbone usually disappears and the loss of ribs and small elements of limbs increase: individuals with a body weight near 200 kg preserve between 40% and 20% of the ribs and between 10% and 20% of the limb small bones, while those near 65 kg preserve less than 10% of the bones of both parts. Within this rank, the vulture seasonal activity is combined with the usual activity of wild boars and others terrestrial scavengers.

Type III. The carcasses of animals with a body weight of 5 kg do not experiment any seasonal destruction dependent on vultures; wild boars are the responsible of the more relevant post-mortem processes. The percentage of the skeletal preserved bones (SCIn) do not exceed 10% in phase II, while the rates increase considerably with regard to the last two models, the disarticulation rate comprises values between 18% and 47%, the dispersion rate between 25% and 47% and the bone loss rate between 23% and 40%. Head, trunk and limbs record very unlikely preservation values (SCIn), more than 40% of skulls and less than 10% of limb large bones are preserved, the rest of the carcass usually disappears in this phase.

It is clear that as the animal body weight decreases the disarticulation, dispersion and bone loss speed is higher, that is why the carcass frequency of the lighter animals is very much lower than the heaviest ones, although the first ones usually show a more numerous population and consequently produce more dead bodies. Dispersion and bone loss are especially significantly related to the adult animal size (dispersion rate: r = -0.60; g. l.=10; p=0.047; bone loss rate: r = -0.63, g.l.=10, p=0.037).

The juvenile ungulate carcasses of any body weight suffers a destruction dynamics more intense than that of any adult, even though the body weight of juveniles of one species is similar to that of any adult of another species. It is possible that the ossification degree of juvenile bones facilitates its fast destruction. According to that, I infer that the preservation factor is the bone consistency degree, which at the same time is dependent on the animal age and size. This factor would explain why birds as the storks, with body weights similar to some carnivores, experiment a total destruction in a few hours while in foxes it takes in months.

Body anatomical parts show different ossification degrees in the same phases.

Head bones last more time on a natural ecosystem surface, followed by vertebrae and long bones of limbs (femur, tibia, pelvis, humerus, radius, ulna and metapodial). The reason can be the shortage of head soft parts that a scavenger can use. These parts are of scarce meat benefit and require a great effort to break the skull; other reasons are the isometric shape of the vertebrae which give them resistance and the disposition of meat around the long bones making unnecessary and scarcely profitable the bone fragmentation.

These general trends can suffer a distortion by some incidents of the physical environment, especially by the intensity of water transportation and by the ecosystem lithological characteristics.

1.- During periods of intense rain, scrubland areas (or 'cotos') where there is no vegetation holding the sand, immediate burials can be produced and complete bodies are preserved. However in those areas with soils reinforced by the vegetation, water currents or temporal flooding do not affect the scattered bone disposition until the land suffers a drought, then the terrestrial scavengers act again increasing bone loss and bone dispersion.

2.- Rabbit bone remains were found on the warren mouths or some few meters from it. We observed that the preservation probability of a rabbit carcass is less than a few hours, so we infer that these remains came from inside of the warren and that they had been taken out by the rabbits when they cleaned these places during each occupation.

Based on the knowledge of the 'fossil potential' of some species from the Doñana community the thanathocoenosis age of each species and of each anatomical part of the carcasses has been estimated; because we understand that the trend showed by the bone deposit, referred to the preservation differences of the carcasses according to individual body weight, does not allow to give a mean age of the complete whole as Behrensmeyer & Boaz (1980) did in the Amboseli Park. We infer from the results obtained that the thanathocoenosis of the Doñana terrestrial macromammals sampled between February 1989 and April 1991 is composed of individuals that died between a date close to the sampling date and more than 29 months before. The Fallow deer would be composed of a higher number of recently dead individuals than those of the Red deer. The youngest bone assemblage is that of the foxes, with less than 11 months of carcass exposition on the Doñana surface.

1.- The bone assemblage of sampled cows have more than 29 months. These cows show an average preservation (SCIn) of 35.2% of the total of their skeletal bones; while the four cows monitored between 16 and 27 months do not exceed the 48%. Also, the 54.3% of head, the 37.8% of trunk, and the 29% of limb bones are preserved.

2.- Three horses monitored during 29 months registered less skeletal preservation than the mean of the eight horses located in the sampling, 50.9% of preserved bones. This means that the horses thanathocoenosis age is less than 29 months, in this time the adult SCIn was of 42.2% and of 37.7% for young mares. Horses located during the sampling preserved 84.7% of head bones, 42% of trunk bones and 54.1% of limb bones.

3.- The average of skeletal preservation obtained in 19 Red deer located during the sampling indicate that the age of the assemblage varies from six months to three years according to the results obtained from the five monitored Red deer. The 18.9% of the head bones was still preserved, as well as 14.7% of those of the trunk and 13.2% of those of the limbs.

4.- According to the 'fossil potential' of monitored Fallow deer, the bone assemblage age of the 31 located Fallow deer would vary from five to 18 months. 44.6% of head bones, 37% of trunk bones and 37.2% of limb bones were preserved.

5.- The bone assemblage of wild boars would exceed sixteen months as obtained by comparing 5% of preserved bones with the fossil potentialities of the three wild boar specimens monitored. Preserved bones represent 57% of the head, 2.2% of the trunk and 1.5% of the limbs. These differences with Fallow deer, which are similar in body weight, is due to the wild boar extractions carried out in Doñana during 1987. The hunted individuals were beheaded on the DBR, and the heads were abandoned, while the bodies were taken to the slaughterhouse.

6.- The age of the bone assemblage of foxes would be less than 11 months according to the 'fossil potential' exhibited by the monitored fox during this period (19.9% for the assemblage, and 6% for the monitored fox). In this assemblage, 71.1% of the head bones, 20% of the trunk bones, and 14.7% of the limb bones were preserved.

CONCLUSIONS

In brief, the observed general destruction dynamics versus the preservation dynamics in Doñana thanathocoenosis allow us to advance in some concepts, methods and interpretations of Palaeoecology and Biology. We can consider the following conclusions:

1.- The bone as preservation unit. I have already mentioned that to measure the preservation of a bone assemblage using the number of preserved individuals ('fossil potential') requires to know some variables of extant populations (yearly turnover rates, death dates) which frequently are unknown. In these cases, we suggest to recognize the 'fossil potential' of the set, through the relationship between the preservation status of carcasses as measured by the percentage of preserved bones of their skeletons (SCIn) and the elapsed time since their deaths.

2.- The assessment of a species presence must be quantified through the temporal preservation status of carcasses which takes account the minimum number of individuals and the differences in the number of bones that form the skeletons of the different species. Such a consideration affect the applied methodology in biostratinomic studies as well as in that of archaeological sites, where the number of remains is continuously used to assess species importance, without paying attention to the preservation degree of its individuals.

3.- The argument cited above is equally applied in the representation and persistence assessment of each anatomical part of the body, which show a significant variation between the individuals of different species and also involving variations in fossilization possibilities.

4.- A general model of body destruction. Measured variables in monitored post-mortem processes give us some general preservation patterns which can be applied to the interpretation of fossil status; in this way, we could know the phase in which the carcass was buried, and the conditions that existed prior to the formation of the taphocoenosis.

5.- The importance of expressing bone loss rate or disappearance body rate in the estimate of mortality and turnover rates as used in Population Dynamics. In Margalef (1989), I have observed in the equation about the relationship between demography, turnover rate and energy flow that the number of deaths, without specifying carcass status, is used: $a = r - m = \log e\ (S+N / S+M)$, for 'a' turnover rate, 'r' increase rate, 'm' mortality rate, 'S' survivors number, 'M' number of deaths, and 'N' birth rate. When estimating M, if only complete or recent carcasses of species with body masses lower than 50 kg are counted, we will underestimate this parameter, because in less than a year their carcasses present a preservation state variability of their skeleton bones between 0% and 100%, e.g. when we found some fox bones, and not just skulls, we must consider them as dead less than a year ago. On the contrary, we may overestimate M if we consider more or less complete carcasses as recent deaths; e.g. carcasses of cows and horses can remain almost complete after five months if they did not die between the end of the Summer and the beginning of the Autumn, and a preservation degree of the skeleton over the 50% will occur after one year of exposition. This would overestimate the mortality of that species in that year.

6.- Fluctuations in the bone loss rate, dispersion rate and disarticulation rate of the remains, as well as the selective preservation of the anatomical parts, are all indicators of biotic and abiotic destructive activity which is continous in an ecosystem. Their values may vary depending of biological conditions.

In order to interpret correctly the past using the preserved fauna in deposits we will have to study the dynamics of the formation of bone assemblages in both natural and human cultural conditions. The present work has presented the methodology to analyse an organic deposit in a determined natural ecosystem. It remains to be known the differences with other ecosystems located in different latitudes to define the general model followed during the formation of a bone deposit, and the particularities of each one of them as the result of interacting agents, including man.

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