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Age-Frequency Profiles in Micromammals: A Methodological Epiphenomenon?

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ABSTRACT: Using an archaeological black rat (*Rattus rattus*) assemblage from a medieval site in Portugal, three age-estimation criteria have been applied in an effort to highlight their influence on the mortality profiles produced. These analyses evidenced different techniques producing different results both in terms of cohort frequency distributions and of the mortality spectra derived from them. A thorough understanding of the biology of living populations proves to be an indispensable tool when attempting to make inferences about the agents, whether cultural, biological or taphonomical, producing specific mortality profiles in archaeological assemblages. Although our results stress the risk involved in the construction and interpretation of mortality patterns from non-recent populations in the absence of data from modern analogues, it is concluded that the application of more than one technique on a particular sample may help circumvent some of the drawbacks inherent to each method when used in isolation.

KEYWORDS: ARCHAEOZOOLOGY, AGE-FREQUENCY PROFILE, MORTALITY, BLACK RAT, *Rattus rattus,* PORTUGAL, MIDDLE AGES

RESUMEN: El trabajo presenta los resultados de la aplicación de tres diferentes métodos de estimación de la edad sobre una muestra portuguesa de rata negra (*Rattus rattus*) de época medieval en un intento por comprobar su influencia en la determinación de su patrón de mortandad. El estudio evidencia que diferentes métodos producen diferentes resultados tanto en lo que se refiere a la abundancia relativa de cohortes como a los espectros de mortandad que de ellas derivarían. Un profundo conocimiento de la biología de las poblaciones actuales parece constituir un elemento clave cuando uno trata de inferir las causas, ya sean éstas culturales, biológicas o tafonómicas, que generan determinados perfiles de mortandad en una fauna arqueológica. Si bien nuestro estudio advierte del riesgo de inferir y valorar patrones de mortandad en poblaciones pretéritas en ausencia de datos actualísticos, también concluye que la aplicación de más de un método sobre una misma muestra ayudaría a neutralizar no pocas de las limitaciones que cada método genera al utilizarse de modo aislado.

PALABRAS CLAVE: ARQUEOZOOLOGÍA, PERFILES DE FRECUENCIA DE COHORTES, MORTANDAD, RATA NEGRA, *Rattus rattus,* PORTUGAL, EDAD MEDIA

INTRODUCTION

Demographic studies in fossil mammals are a powerful tool in the hand of the paleobiologist, despite some inherent difficulties related to sample size and limitations concerning the use of modern inferential analogues (Kurtén, 1983; Klein & Cruz Uribe, 1984). Several analyses carried out on various rodent species, demonstrate that age-frequency profiles based on tooth crown wear are essentially identical to those found in larger brachydont carnivores and hypsodont herbivores (Korth & Evander, 1986; Bryant, 1991). In the case of small, short-lived, brachydont mammals cohorts can be evidenced provided: (1) sufficiently large samples and (2) demonstrable seasonality in breeding cycles are found in the populations under analysis (Flemming, 1971; Bryant, 1991). Still, as these authors and others stressed, the conformity of mortality profiles to either attritional or catastrophic models may at times be quite misleading, a point of great relevance in view of the importance laid on mortality patterns by paleoecological studies.

In the present paper, the possibility of identifying catastrophic versus attritional profiles is addressed from the strictly methodological standpoint of evaluating the differences that three different age-estimating methods bear on the configuration of a particular profile for the same «population». If certain biological features of the species under analysis are masked by the analytical tools used to study them, we could eventually obtain results whose explanations might be attributable to both proximate and ultimate causes, a matter of concern for future studies.

MATERIALS AND METHODS

The black rat (*Rattus rattus)* assemblage that we present here was retrieved in a sealed cesspit on the floor of a house at the site of Mertola (Baixo Alentejo, Portugal) dating back to Almohad times (i.e., early XIIIth century AD; Morales, 1993; Morales & Rodríguez, 1997). Both the cesspit and the sediment lying above the floor were sieved through a fine (1-2 mm) mesh. In the cesspit, abundant microvertebrate debris (mostly fish) as well as marine shells, indicative of kitchen refuse and leftovers, was found. The most remarkable find was the presence of a potential rat predator, the genet (*Genetta genetta*) which constitutes the earliest and only evidence of this viverrid in the european paleontological record (Morales, 1994). Faunal remains in the Telhado (i.e. floor) unit were scarce and essentially restricted to the reported rat finds. A previous taphonomic analysis concluded that this rat assemblage had been the result of natural deaths rather than an accumulation of predated animals (Morales & Rodríguez, 1997).

Several papers (eg., Bryant, 1991) have stressed that, in order for discrete age-groups in mammalian deposits to appear, a pattern of seasonal breeding is required. The commensal habits of the black rat have apparently disrupted its original breeding pattern so that, today, most of them breed throughout the year. However, we do not know when this disruption took place (Ervynck, 1989; Armitage, 1993; Audoin-Rouzeau & Vigne, 1997). What we do know is that black rats were originally seasonal breeders, and that this shift cannot be too old for, even today, most breeding in London occurs from mid-March to mid-November (Davis, 1953; Corbert & Harris, 1991). Likewise, seasonal fluctuations in breeding intensity have been described as ‘marked’ in Cyprus, with peaks in April and September and lows during the month of January (Watson, 1950). Additional information necessary for the calculation of demographic profiles comes from several studies that provide data on the growth pattern of this rodent allowing us to make age-estimations based on size and weight parameters from present-day populations (Watson, 1950; Davis, 1953; Bentley & Taylor, 1965; Corbert & Harris, 1991).

Body size and body mass in this paper have been estimated from Zamorano *et al.* (1986) as follows:

$$\text{Weight} = 3.44 \text{ x } 10^{-4} \text{ x ML}^{4.06} \quad (1)$$

$$\text{Size (head + body length)} = 34.35 \text{ (ML-12)}^{0{,}67} \quad (2)$$

where ML corresponds to mandibular length (Figure 1).

These authors confirm a good correlation between expected and observed values, taken from samples covering a wide range of ages from infant to old adult. One should stress that all of the rat samples taken into consideration for those analyses came from Andalusia, a southern Spanish territory in contact with the portuguese province of Baixo Alentejo, where Mertola is located. This is an often overlooked aspect since, for species which, like *Rattus rattus*, tend to exhibit a «patchiness» in their local distribution that favours divergence and the development of local varia-

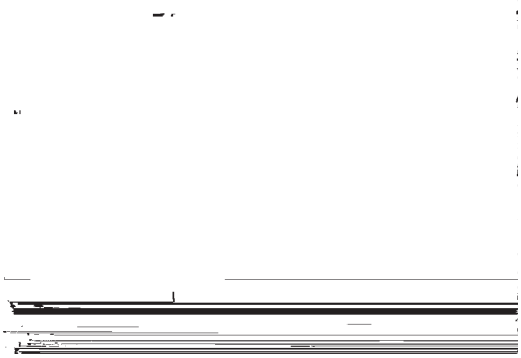

FIGURE 1

Measurement of the mandibular length, ML, as defined in this paper (i.e., from the most oral dorsal margin of the incissor's alveolus to the aboral margin of the articular process).

tions, inferences of this kind should be based on sets of data from populations as similar as possible to the ones being investigated. Both Miller (1912) and Cabrera (1914) have confirmed, for example, that Iberian black rats are smaller than those from other European populations, and this has been confirmed by our previous metrical results (Morales & Rodríguez, 1997) reinforcing our confidence in the applicability of equations (1) and (2) to our Mertola case study.

In a previous analysis (Morales & Rodríguez, 1997), the black rat assemblage was subdivided into cohorts by the use of a continuous-unit method (i.e., measurement of the mandibles) and by two discrete-unit methods, namely: (1) a tooth wear calendar developed by Armitage for the upper cheek teeth and (2) the allocation of weight estimates into the «cohorts» (weight categories) proposed by Bentley & Taylor (1965). Although in the later case the sample population, reared in the laboratory, might not be prove so adequate an analogue for our archaeozoological samples, one would expect the amount of variation implicit in these authors' categories (Table 2) to amply exceed small weight discrepancies between both data sets.

In addition, for the present study, a series of measurements were taken on both the upper and lower first and second molars to further refine the degree of resolution that the mandibular length estimations hinted at and to check whether or not the mortality profiles evidenced by our previous analyses held. These measurements include:

a) Essentially age-independent parameters such as crown lengths (Figure 2A, l) and widths (Figure 2A, w).
b) Essentially age-dependent parameters as is the case for crown heights (Figure 2A, h) from specific cusps. In the upper first molar (M^1) these cusps were conventionally labelled «X'», «6» and «Z» (Figure 2B), whereas those of the upper second molar (M^2) were labelled «6» and «Z» (Figure 2B). For the lower first molar (M_1), the selected cusps were labelled «TD», «TE» and «TF» (Figure 2C) and those of the lower second molar (M_2), «TD» and «TF» (Figure 2C).

Although these measurements cannot be automatically translated into an absolute age-profile, their age-dependency should at least allow one to test the validity of the previously obtained cohort profiles from an independent standpoint.

All measurements were made with a Wild-Heerbrugg ocular micrometer, at 50X magnification, accurate to 0.04±0.02 mm. Standard univariate statistics have been incorporated in all instances. For the various osteometrical parameters we additionally calculated the coefficient of bimodality (B) defined as:

$$B = (m_3^2 + 1)(m_4 + 3) \qquad (3)$$

CHARACTER	N	Ȳ	OR	SD	SE	V	CV
ML	18	21.8	16.9-28.6	2.31	0.55	5.36	10.59
Weight (g)	18	100.9	33.9-281.5	51.02	12.02	2602.6	50.55
Head + Body (mm)	18	158.9	100.7-225.6	24.76	5.84	613.21	15.67

TABLE 1

Univariate statistics for mandibular length, ML, as defined in Figure 1 and corresponding weight and size (i. e., head + body length) estimations of the *Rattus rattus* sample from Mértola. Ȳ=Mean; OR=observed range; SD=standard deviation; SE=standard error; V=variance; CV=coefficient of variation; N=sample size.

WEIGHTS (g)	MNI (ML)	COHORT	AGE
30-40	1	Infantile	3 weeks ≈
60-70	3	Juvenile	
70-80	1	Juv/Subadult	(1)
80-90	4	Subadult	8-12 weeks
90-100	1	Young adult	(2)
100-110	3	Adult	
110-120	2	Adult	
120-130	2	Adult	
280-290	1	Old adult	(3)

TABLE 2

MNI of *Rattus rattus* allocated to specific, 10g-weight interval groups corresponding to particular cohorts [(1) molar eruption completed around 80 g (± 10 g) in *R. norvegicus* for ML values of 20-21 mm (Morris, 1979); (2) maturity reached on, on the average, around 11 weeks but female mature earlier than males (Bentley & Taylor, 1965); (3) one female reached 260 g at 957 days of age; an old male reached 305 g at 428 days (Bentley & Taylor, 1965).

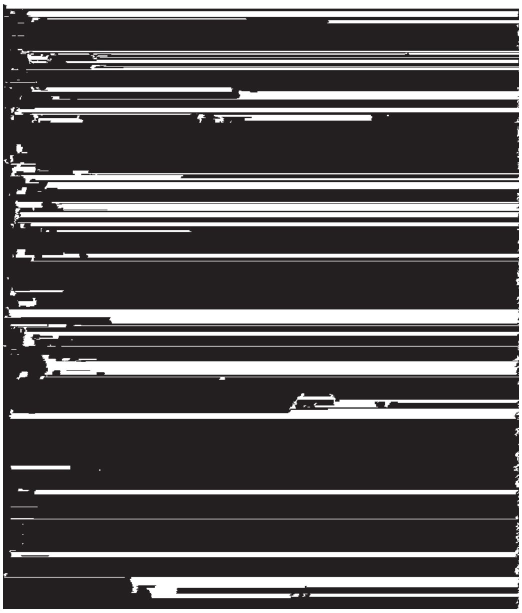

FIGURE 2

Dental measurements. A. Idealized molar: both width (i.e., greatest labio-lingual dimension, w) and length (i.e.,greatest oro-aboral dimension, l) are taken at neck level (i.e., the constriction between crown and root). Height (h) ranges from neck level to the abraded surface of a particular cusp. B. Cusp nomenclature for the upper first (M1) and second (M2) left molars. C. Cusp nomenclature for the lower first (M1) and second (M2) left molars (B and C taken from Armitage in Morales & Rodríguez, 1997).

Where m_3 indicates skewness and m_4 kurtosis. Values greater than 0.555 are here taken to indicate bimodal or polymodal distributions (SAS Institute, 1985: 272). Finally, a correlation matrix, subdivided into maxillar and mandibular samples, was calculated for all the measurements taken into consideration, in order to explore to what extent, if any, were any particular variables linked to others (Tables 4 & 5).

Identification was originally carried out with the help of the reference specimens housed at the Laboratorio de Arqueozoología of the Universidad Autónoma de Madrid, though occasional use was made of criteria reported in the literature (*e. g.* Wolf *et al*., 1980). In those cases where the identification was not feasible below genus level, as is the case of juvenile and extensively fragmented specimens, and also in view of the essentially post-medieval occurrence of the brown rat (*Rattus norvegicus*) in Europe (Heinrich, 1976; Ervynk, 1989; Armitage, 1993; Audoin-Rouzeau & Vigne, 1997), remains were parsimoniously assigned to *R. rattus*. Due to the high probability that the sample included complete specimens, and in order to neutralise potential duplications of individuals, the MNI (minimum number of individuals) was used as the abundance estimator (Badgley, 1986). Still, even within this sealed context and finely excavated samples, it appears that each mandible belonged to a different individual, reinforcing Gautier's now classic claim regarding the generally negligible effects of interdependence on most archaeozoological samples (Gautier, 1984).

RESULTS

A. *Tooth wear calendar*

The application of Armitage's tooth wear calendar to the sample indicated an almost exclusive

CH	Mean	OR	SD	Skew.	Kurt.	B	CV	N	Z	α
Maxilla										
M1 L	2,75	5,53-2,93	0,12	-0,13	-1,04	0,52	0,04	18	0,69	0,73
M1 W	1,93	1,83-2,03	0,07	-0,03	-1,16	0,54	0,03	18	0,58	0,89
M1 6	0,87	0,59-1,05	0,13	-0,76	0,14	0,50	0,15	18	0,61	0,85
M1 x	0,79	0,47-1,05	0,15	-0,59	0,25	0,42	0,18	18	0,77	0,59
M1 z	0,87	0,55-1,17	0,16	-0,16	0,58	0,29	0,18	18	0,88	0,42
M2 L	1,72	1,56-1,91	0,10	0,06	-0,39	0,38	0,06	15	0,50	0,96
M2 W	1,80	1,68-1,95	0,09	0,47	-0,77	0,55	0,05	15	0,66	0,77
M2 6	0,83	0,59-0,94	0,10	-1,67	2,33	0,71	0,12	15	1,04	0,23
M2 z	0,82	0,47-0,98	0,13	-1,67	3,97	0,55	0,15	15	0,92	0,37
Mandible										
M1 L	2,905	2,78-3,06	0,078	0,12	-0,804	0,46	2,69	18	0,698	0,715
M1 W	1,583	1,40-1,75	0,111	-0,19	-0,914	0,50	7,01	18	0,555	0,918
M1 TD	1,019	0,78-1,22	0,146	-0,368	-1,295	0,67	14,33	18	0,663	0,772
M1TE	1,04	0,78-1,25	0,155	-0,436	-1,144	0,64	14,90	18	0,675	0,753
M1 TF	1,004	0,75-1,28	0,135	0,152	-0,286	0,38	13,45	18	0,617	0,841
M2 L	1,808	1,65-1,93	0,076	0,12	-0,11	0,35	4,20	18	0,876	0,427
M2 W	1,754	1,62-1,90	0,083	0,129	-1,008	0,51	4,73	18	0,546	0,926
M2 TD	1,09	0,84-1,31	0,14	-0,255	-0,96	0,52	12,84	18	0,631	0,821
M2 TF	1,09	0,84-1,31	0,138	0,051	-1,014	0,50	12,66	18	0,620	0,836

TABLE 3

Univariate statistics (with linear values expressed as milimeters) of the upper and lower M1 and M2 of *Rattus rattus* from Mértola. Abbreviations as follows: CH=character; OR=observed range; SD=standard deviation; Skew.=skewness; Kurt.= kurtosis; B=coefficient of bimodality (see equation (3) in text); CV=coefficient of variation; N=number of observations; Z=Kolmogorov-Smirnov test Z-value; α = significance level of the K-S test. M1L & M2L = length of particular tooth at crown level; M1 W & M2 W = width of particular tooth at crown level. All other osteometrical parameters refer to crown height at specific cusp levels (for cusp nomenclature and definition of particular crown heights see Figure 2). Other abbreviations as in Table 1.

	M1 6	M1 Z	M1 W	M1 L	M1X'	M2 6	M2 W	M2 L	M2 Z
M1 6	1 —								
M1 Z	0,942 P=0,000	1 —							
M1 W	0,420 P=0,135	0,330 P=0,249	1 —						
M1 L	0,383 P=0,177	0,369 P=0,194	0,862 P=0,000	1 —					
M1 X'	0,929 P=0,000	0,919 P=0,000	0,401 P=0,155	0,401 P=0,155	1 —				
M2 6	0,591 P=0,43	0,678 P=0,15	0,353 P=0,260	0,414 P=0,181	0,733 P=0,7	1 —			
M2 W	0,000 P=1,000	-0,076 P=0,815	0,608 P=0,36	0,572 P=0,52	-0,102 P=0,752	-0,027 P=0,933	1 —		
M2 L	0,271 P=0,394	0,268 P=0,400	0,864 P=0,000	0,751 P=0,5	0,170 P=0,597	0,198 P=0,537	0,792 P=0,2	1 —	
M2 Z	0,775 P=0,3	0,866 P=0,000	0,445 P=0,147	0,429 P=0,164	0,883 P=0,000	0,661 P=0,19	-0,147 P=0,648	0,260 P=0,415	1 —

TABLE 4

Correlation matrix of maxilar characters (Character codes as in Figure 2 and Table 3).

	M1 W	**M1 L**	**M1 TD**	**M1 TE**	**M1 TF**	**M2 W**	**M2 L**	**M2 TD**	**M2 TF**
M1 W	1 —								
M1 L	0,529 P=0,24	1 —							
M1TD	0,115 P=0,650	0,266 P=0,287	1 —						
M1TE	0,103 P=0,685	0,387 P=0,113	0,969 P=0,000	1 —					
M1TF	0,195 P=0,438	0,303 P=0,221	0,915 P=0,000	0,872 P=0,000	1 —				
M2 W	0,859 P=0,000	0,721 P=0,1	0,223 P=0,374	0,301 P=0,225	0,297 P=0,231	1 —			
M2 L	0,073 P=0,773	0,437 P=0,70	-0,115 P=0,649	0,036 P=0,888	-0,222 P=0,376	0,219 P=0,382	1 —		
M2TD	-0,268 P=0,283	0,116 P=0,645	0,799 P=0,000	0,825 P=0,000	0,686 P=0,2	0,026 P=0,919	-0,146 P=0,564	1 —	
M2TF	-0,259 P=0,299	0,054 P=0,832	0,741 P=0,000	0,757 P=0,000	0,631 P=0,5	-0,009 P=0,972	-0,158 P=0,531	0,965 P=0,000	1 —

TABLE 5

Correlation matrix of mandibular characters (character codes as in Figure 2 and Table 3).

presence of «young adults» (stage 4) (Figure 3; Morales & Rodríguez, 1997). Only one specimen was recorded as belonging to stages 5 (i.e., «adult») and 6 («old adult»), thus providing a strongly unimodal distribution of cohorts which, due to the abundance of «middle-age» individuals, best conformed to a micromammal catastrophic mortality profile (Korth & Evander, 1986: 233).

B. *Size/weight estimates*

Standard univariate statistics for mandible lengths (ML), as well as for length and weight estimates appear in Table 1. Table 2 allocates such estimations, expressed as specimens (MNI), within Bentley & Taylor's age-weight categories and Figure 4 plots the resulting mortality profile. Although still clearly unimodal, the presence of additional cohorts renders unimodality less marked than in the case of the tooth wear calendar and reveals juveniles as the modal cohort. One might argue that such differences are attributable to either the different data sets (i.e., mandibles vs. upper tooth rows) or the nature of the methods involved (i.e., qualitative vs. quantitative) but there might exist at least two additional phenomena, biological and methodological that help explain these discrepancies:

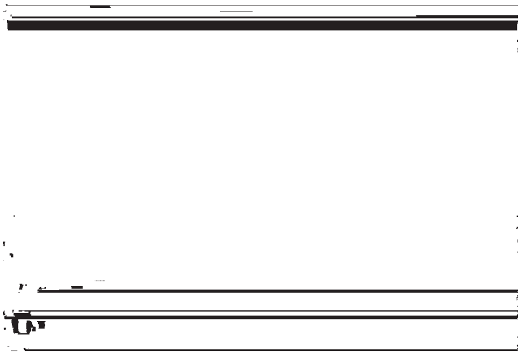

FIGURE 3

Mortality profile of the black rat sample from Mértola as evidenced by the application of the upper molar wearing stages defined in Morales & Rodríguez (1997). Cohort codes: 4=young adult, 5=adult, 6=old adult.

a) Biological. Tooth wear proceeds at a variable rate during ontogeny, being fastest when the tooth becomes functional and progressively slowing down as tooth surfaces become smoother. This phenomenon holds for both brachydont and hypsodont teeth of macro

FIGURE 4

Plotting of the data in Table 2. Cohort codes: Inf=infantile, Juv=juvenile, Juv/sa=Juvenile/Subadult, S.adl.= subadult, Y.adl.= young adult, Adl.=adult, O.ad.=Old adult.

> –and micromammals (Payne, 1973; Djamchid, 1978; Grant, 1982, Levine 1982), and implies that early wear stages are short-lived, standing a smaller chance of being retrieved. It also means that, somatically speaking, an animal may be younger than its toothwear pattern would suggest if, for example, its diet happens to be a particularly abrasive one (Morris, 1972; Hewison *et al*., 1999). Therefore, unless one is able to assign reliable temporal margins to specific wear patterns, the discrete cohorts offered by any particular tooth wear calendar might prove much too coarse a tool for demographic analysis of populations in general or for inference of mortality profiles in particular (Klein *et al*., 1981; Klein, 1982; Klein & Cruz-Uribe, 1983).

Weight and size increases, on the other hand, seem to be more gradual phenomena, and from what the mandible data suggest, parameters that correlate with age until the death of most animals. This fact, in view of the determinate nature of mammalian growth (Klein & Cruz-Uribe, 1983), seems paradoxical but might be explained, at least in the case of rats, by the fact that most animals die well below their potential longevity threshold thus probably before their somatic development reaches its levelling phase (Bentley & Taylor, 1965; Korth & Evander, 1986; Damuth & MacFadden, 1990). As a substantiation of this statement, it should be noted that the majority of the black rat postcranial remains in our sample featured unfused epiphyses (Morales & Rodríguez, 1997).

b) Methodological. By mere virtue of design, the inferential estimation of weight/size produces a continuum of values and, consequently, a higher degree of resolution (i.e., a potentially higher number of categories into which specimens can be allocated) than is the case for the tooth wear calendar. By virtue of design, then, the «weight-assignal» method would reduce the probability of producing a highly skewed distribution of items without the need of resorting to less parsimonious explanations.

C. *Teeth measurements*

Standard univariate statistics for crown lengths, widths and heights appear in Table 3. Figures 5-8 plot the distribution frequencies for each isolated parameter. None of the age-dependent (i. e., height) characters are significantly skewed or kurtotic at 0.05 confidence, using a two-tailed test (Sokal & Rohlf, 1981). Furthermore, all variables conform to a normal distribution at a 0.05 confidence level (Table 3). The values of the Coefficient of Bimodality (B), although close to bimodality/polymodality values in many of the mandibular teeth parameters, are only clearly so in the case of the M^1 age-independent characters and in two of the three age-dependent ones for the M$_1$, namely the heights of the TD and TE cusps (Table 3; SAS Institute, 1985). Ideally, in this univariate analysis, cohorts should be represented by distinctly bimodal (representing two cohorts) or polymodal (representing multiple sympatric cohorts) distributions in crown height measurements (Voorhies, 1969; Kurtén, 1983). In this case, despite the comparatively small size of our samples, some of the values indeed indicate: (1) the existence of cohorts and (2) the possibility of revealing these for particular teeth (i.e. M^1, and M$_1$) through the use of osteometrical variables. Such results reinforce one of the conclusions from our previous study (Morales & Rodríguez, 1997) while stressing the weaknesses inherent to the database for determining whether a putative natural «tanatocenosis» (i.e., death assemblage) was the result of a catastrophic or an attritional mortality event.

Figures 5-8 further evidence that not all of the characters behave in the same manner, some exhibiting more polymodality (Figure 5B), others being more bimodal (Figure 7E). In general, all are more or less skewed towards lighter wear. In particular, the height of cusp «6» in the M^2 seems to be clearly bimodal (Figure 6C), and indeed its B-value is well above 0.555 (Table 3).

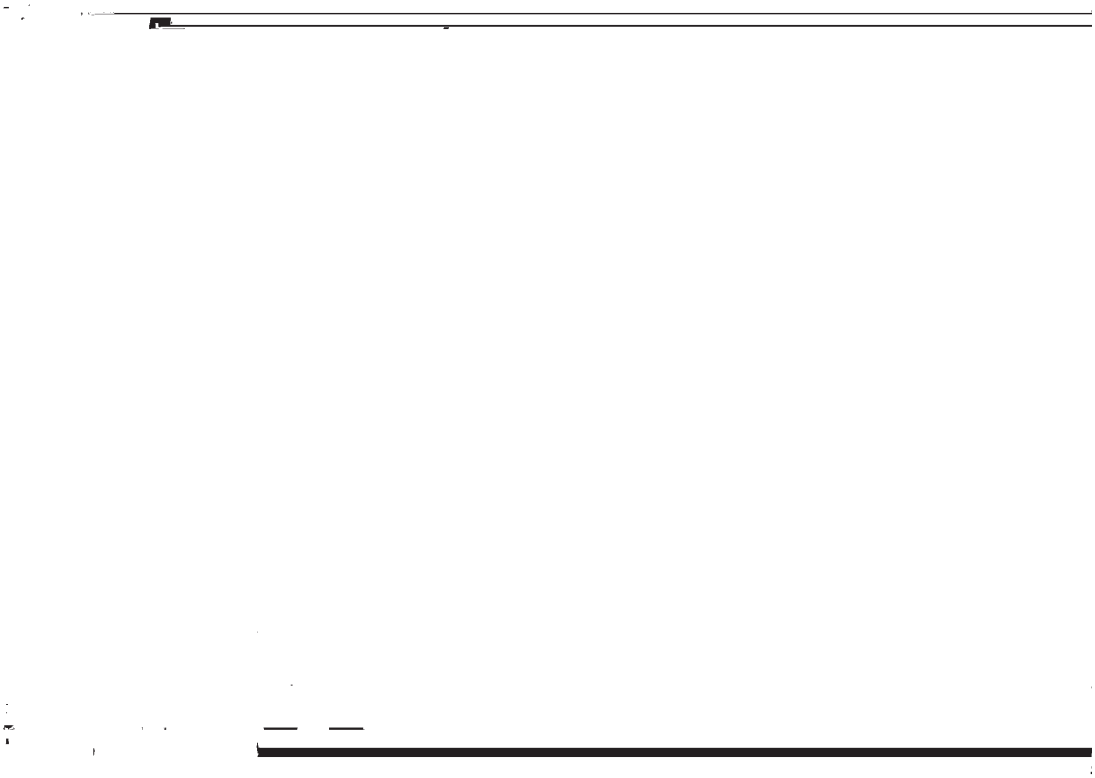

FIGURE 5

Graphic plotting of the frequency distributions of osteometrical characters (expressed in millimeters) recorded on the upper M1. A=L(length), B=W(width), C=height at X’, D=height at Z, E=height at 6.

The coefficients of variation (CVs) seem to fall in all instances within the typical ranges for linear measurements in mammalian populations (Table 3; Gingerich, 1974; Yablokov, 1974; Payne & Bull, 1988; Rowley-Conwy, 1995); the higher CVs of crown height measurements could be

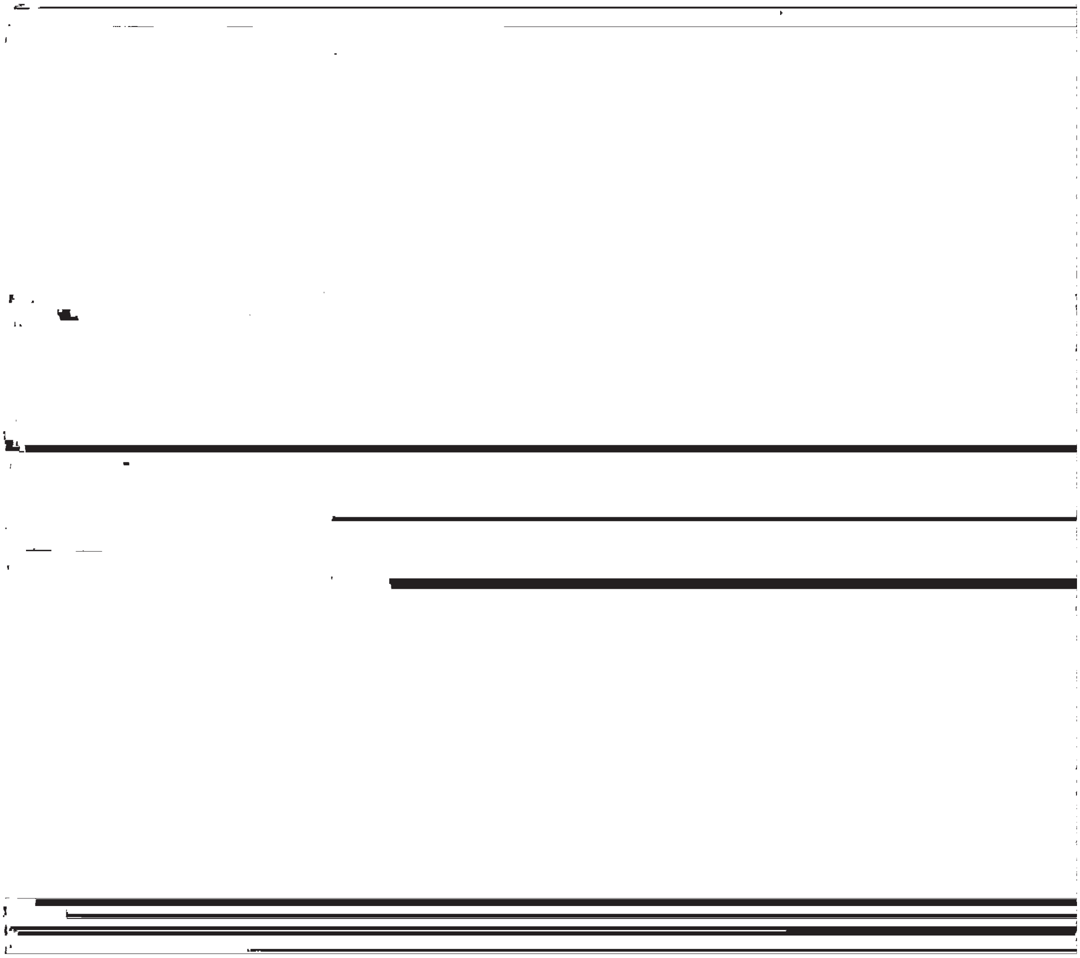

FIGURE 6

Graphic plotting of the frequency distributions of osteometrical characters (expressed in millimeters) recorded on the upper M2. A=L(length), B=W(width), C=height at 6, D=height at Z.

essentially explained by their often higher correlation with age (Hulbert, 1984). Also, as Tables 4 and 5 suggest, all age-independent characters are positively correlated with each other. As expected, the correlation between age-dependent and age-independent characters is very weak and non-significant (Table 3). The variables from the same tooth have a correlation close to 0.90, but the correlation between variables of the M1 and the M2 from the same individual are considerably weaker (Tables 4 and 5). High correlations between age-dependent characters should be taken to indicate: (a) a homogeneous wearing of crowns at all points and (b) an absence of unworn crown heights, a well-known and inherent problem as a source of variation in this kind of studies (Kurtén, 1953). Correlations in the same range of values as the ones seen here (i. e., normally around but not above 0.90) seem to be the norm in the case of ungulates (Klein, 1982; Klein & Cruz-Uribe, 1983, 1984) but, due to the aforementioned drawback concerning unworn crowns, have been found to be lower in the only one instance we know of a fossil rodent species assemblage (Bryant, 1991: 7). If, on the other hand, it is assumed that individual variation in tooth wear rates (and, therefore, of crown height at any particular age) may be high in rodents, as Fleming (1971) recorded in an extant

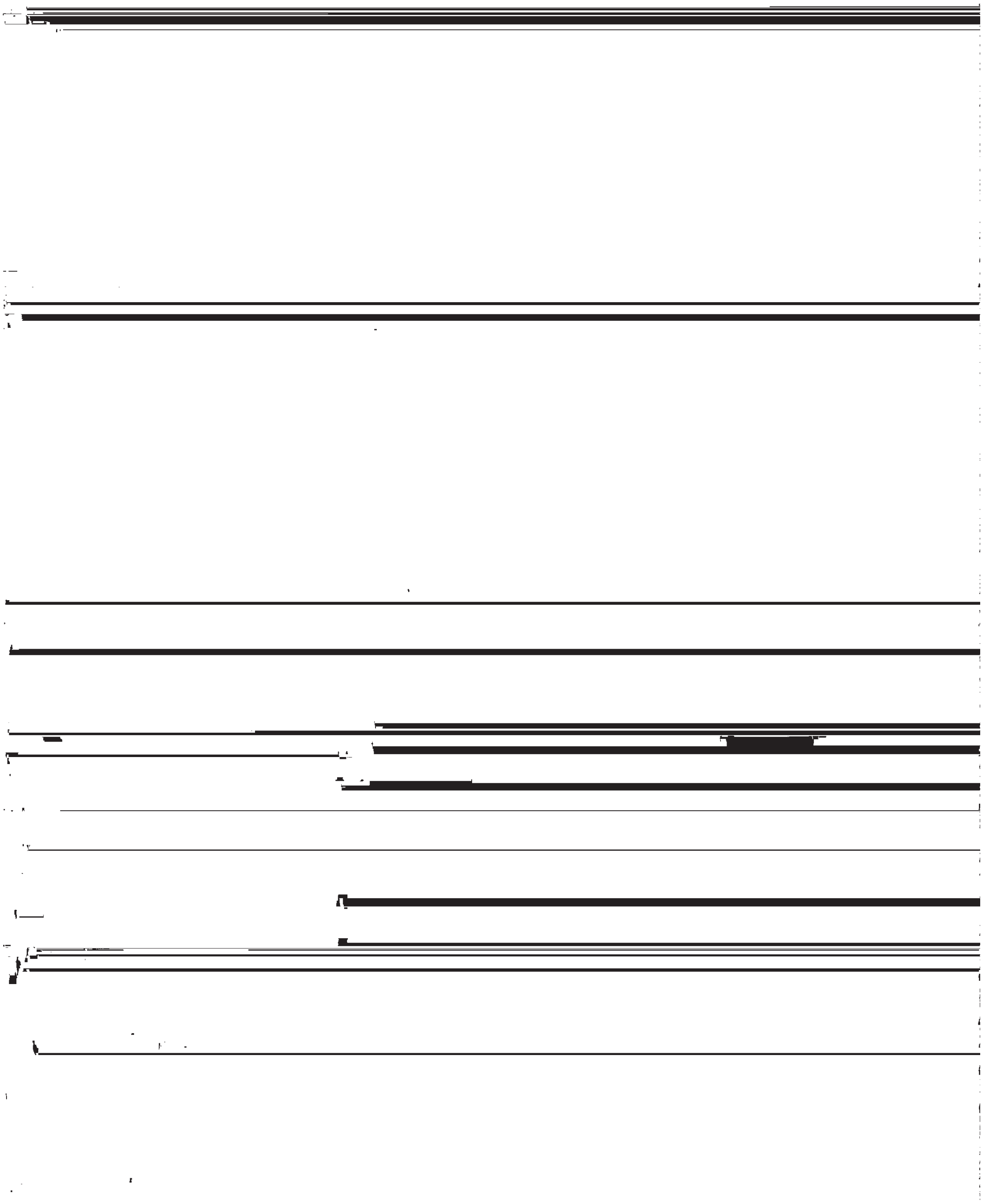

FIGURE 7

Graphic plottings of the frequency distributions of osteometrical characters (expressed in millimeters) recorded on the lower M1. A=L(length), B=W(width), C=height at TF, D=height at TD, E=height at TE.

population of *Lyomis adspersus*, little faith should be laid on the quantitative or qualitative detection of cohorts based on the exclusive use of univariate statistical methods. A cursory look at Figures 5-8 seems to confirm that this might, in fact, be the case here as well.

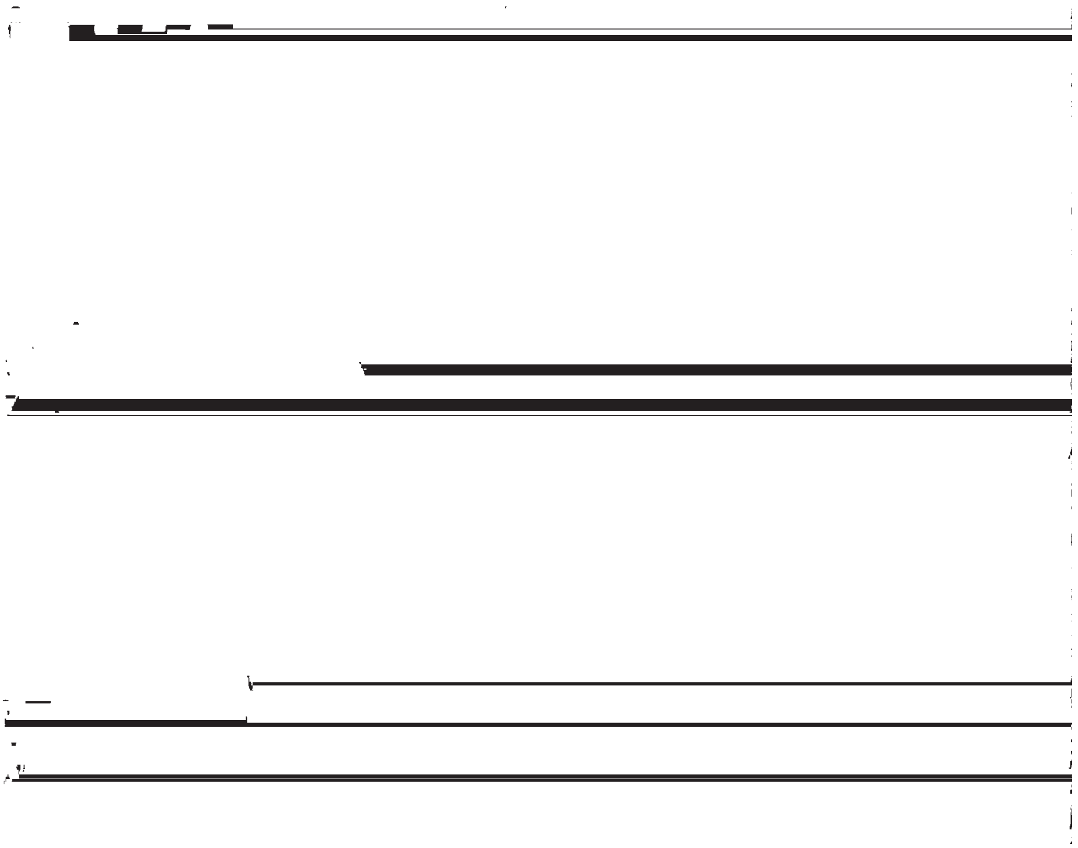

FIGURE 8

Graphic plotting of the frequency distributions of osteometrical characters (expressed in millimeters) recorded on the lower M2. A=L(length), B=W(width), C=height at TF, D=height at TD.

Figure 9 plots the values of crown height variables for teeth in different wear stages. It may seem peculiar that teeth with different wear stages have the same crown height. This is particularly evident in the case of the M^1 (Figure 9A). Such pattern probably arises as a consequence of the variation of crown height values in unworn teeth.

One way or the other, it should be clear that the use of osteometrical parameters enhances the degree of resolution of the previous age-estimating methods. Consequently, whether upper cheek teeth (as was done in the case of the wear calendar) or mandibular teeth are considered, unimodal distributions invariably turn into bimodal/polymodal ones implying that strictly methodological constraints need to be taken into account when attempting any interpretation of mortality profiles.

DISCUSSION

Different authors note that the shapes of mammalian mortality profiles will vary between populations depending upon the biology of the species (Klein & Cruz-Uribe, 1983, 1984). In the case of short-lived species, in which most individuals in a cohort do not survive to the next breeding season, profiles are implicitly assumed to conform to unimodal distributions such as those shown in Figures 3 & 4. The logic behind such patterns seems to be rather straightforward: for animals with life spans in the order of 2-3 years, survivorship (and, hence, cohort definition) occurs at a scale, measured in terms of months, not resolvable when birth and death cycles are seasonal on a yearly interval (Bryant, 1991).

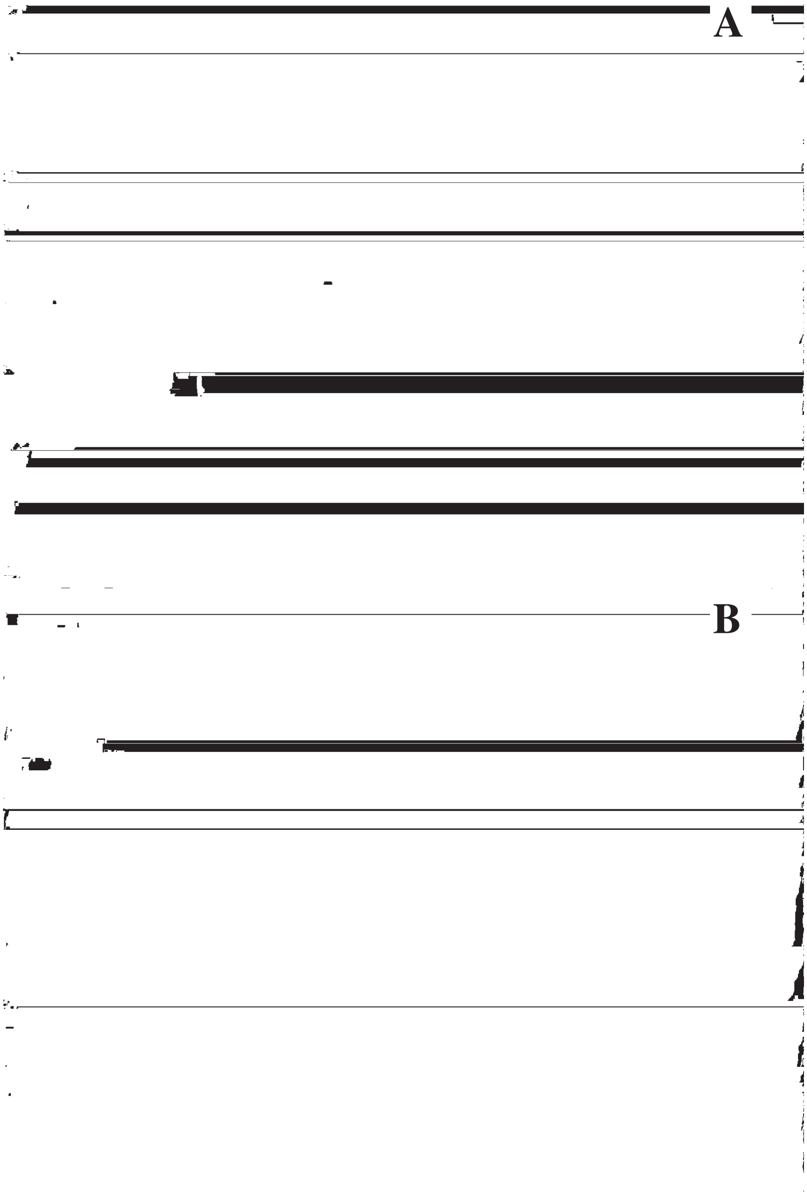

FIGURE 9
Cusp height and wear stage of the M^1 (A) and M^2 (B). Abbreviations as in Figure 2.

Since birth and death cycles are the factors ultimately dictating the abundances of the various cohorts, small mammal populations should not be expected to conform with modelled profiles of either attritional or catastrophic mortalities. Distinction between these requires the recognition of demographic patterns in univariate histograms of an age-dependent character which, at the very least, should include: (1) high juvenile mortality (2) low mid-life mortality and (3) sudden increased mortality of senile individuals (Klein & Cruz-Uribe, 1983, 1984; Korth & Evander, 1986; Bryant, 1991). Notwithstanding what happens in species like black rats, whose life-spans might actually average slightly above the 2-3 year threshold, profiles with an abundance of «middle-aged» individuals are normally taken to indicate a catastrophic type of mortality. However, we know that «intermediate» tooth wear stages are the longest lived and thus stand, on strictly probabilistic grounds, the highest chances of being retrieved in the deposits. Moreover, in the case of certain rodent species, one should also keep in mind that «middle-aged» individuals live more risky lives than those in other cohorts, often being the ones undertaking dispersals from group to group, establishing new territories, and carrying out most of the breeding in the population (Miller, 1912; Cabrera, 1914; Watson, 1950; Davis, 1953; Corbert & Harris, 1991). As a corollary of such phenomenon, one would expect these cohorts to stand the greatest chances of being predated and, eventually, accumulating at a specific spot this being a den, a cesspit, dumpyard or a roosting place for that matter. In this way, two robust arguments combine, for entirely different reasons, for one to expect finding more teeth from young adults in deposits. Under such circumstances, whether a particular age profile could be taken to reflect the real age structure of a former population or the behaviour pattern of a specific predator would remain entirely open to speculation (Andrews, 1990). In the absence of the pertinent contextual information, therefore, how could one infer the nature, whether natural mortality or predated population, of a particular accumulation or to be sure that a specific mortality profile provides meaningful data about the biology of a species?

What happens, moreover, when biological and probabilistic constraints are not the sole agents dictating a particular mortality profile? The various techniques employed in monitoring mortality in this study have incorporated an additional element (i.e., methodological constraints) into the discussion. For paleofaunal studies such proximate factors have been discussed at length in the case of retrieval biases (Payne, 1972; Lyman, 1994) and, within a general context, constitute the essence of Heisenberg's «uncertainty principle» (i.e., «*What we observe is not nature itself but nature exposed to our method of questioning*»), yet none of the authors studying ageing methods seem to have ever gone into much depth when dealing with this potential limitation of the data. The assumption that once a mortality profile has been established on the basis of one technique it will hold under alternative ones seems too logical to resist. Although our analysis was carried out on a rather homogeneous and restricted sample, and inferences should be taken with caution, it nevertheless seems apparent that:

- Different techniques do produce different results with a non-quantifiable, though still obvious, correlation existing between the degree of resolution of the specific estimator and the skewness of the mortality profile it generates (Figures 3-8). In the case of our first two methods, still, one may argue that differences could be attributable to the nature of the osteological sample chosen (i. e., upper *vs*. lower teeth and mandibles).
- Even the same estimator (i.e., crown height) may produce different profiles depending not only on the type of tooth chosen, but also on the choice of cusps within a particular tooth.

Due to the restricted nature of our study it is impossible to determine at this stage to what an extent its results can be extrapolated to other populations of black rats, let alone other species of rodents or mammals. Inconsistencies in the use of age-profile estimates or mortality profiles are to be expected when one considers the wealth of limiting factors inherent to any technique that are still not fully understood. The obvious solution is to combine techniques which may compensate for each other's «weaknesses».

Likewise, context is often the critical issue. In order to highlight its importance, we would like to consider a minor «flaw» implicit in the straightforward application of crown height measurements, the most sensitive of all the non-skeletochronological age-dependent techniques considered thus far. Since this method does not provide point estimates but, rather, a protocole for pigeonholing items into pre-established categories, the critical issue is how does one define such categories. From such standpoint what few authors seem to realise is that in many cases absolute crown height values *per se* are incomplete in that they do not incorporate specimens from the very earliest ontogenetic stages (i.e., dotted lines in Figure 10A). As Levine (1982) evidenced in her seminal work on horse teeth, crown height values from those very early stages, in fact, duplicate crown height values from later stages (Figure 10B) since teeth, whether brachydont or hypsodont, increase in size both *before* and *after* eruption yet erosion only takes place *after* eruption. Maximum crown height is,

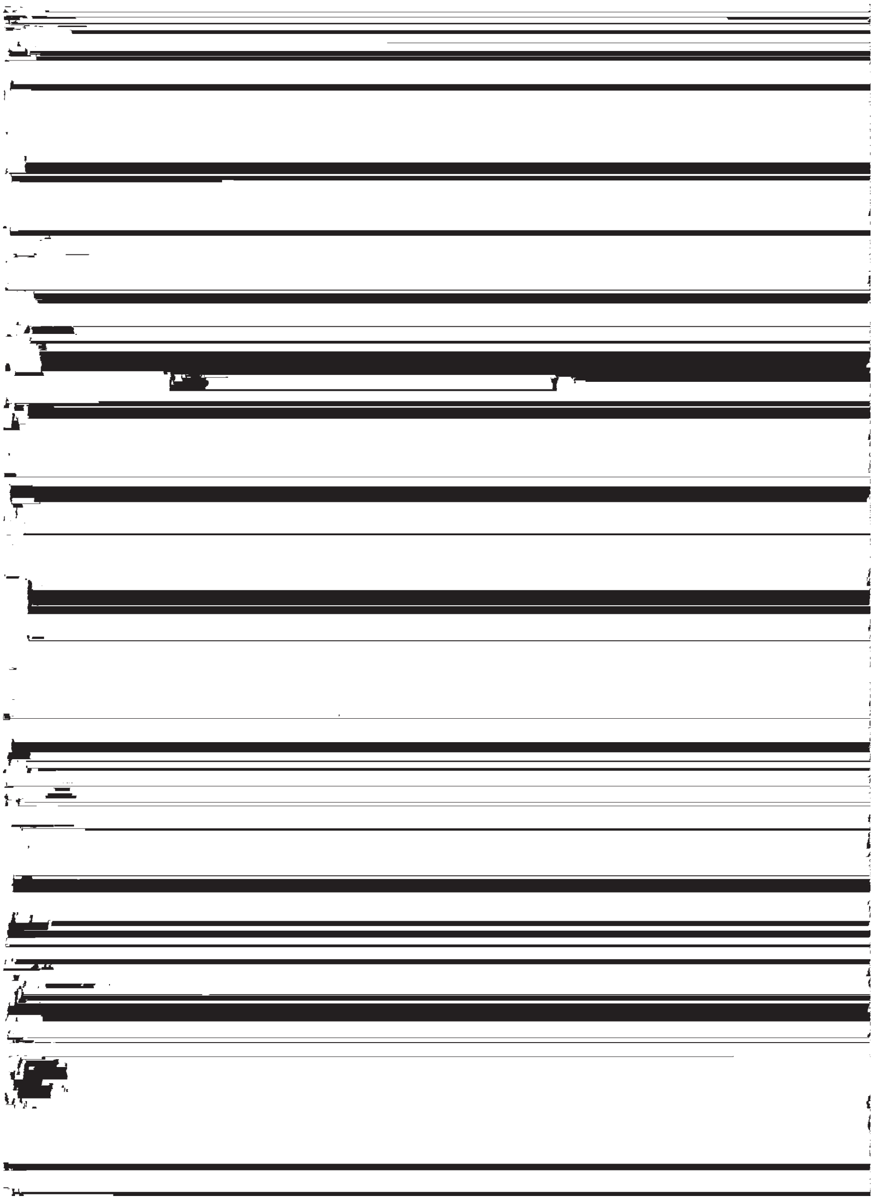

FIGURE 10

A. Evolution of crown height of the upper first molar in *Equus*. For the earliest stages of tooth development (dotted line) crown heights are unknown (taken from Spinage, 1972). B. Crown height values of the permanent upper second premolar throughout ontogeny. The dotted line indicates the moment when the tooth becomes functional. As the tooth develops, crown height values from the earliest ontogenetic stages (a, b, c) duplicate those from later stages (a', b', c'). Taken, with modifications, from Levine (1982).

thus, attained not when the tooth erupts but slightly later (Levine, 1982) and a peculiar symmetry in crown height values arises that may lead into errors when ageing specific items, particularly when applied to isolated or damaged specimens as is often the case in subfossil assemblages. Thus, unless corrective checks, combining crown height values with morphological information that allows one to know to what portion of the curve a specimen belongs, are introduced, erroneous inferences about the age of a tooth, or the cohort to which a particular specimen with a specific crown height value belongs, are bound to result.

From a methodological standpoint, also, such corrective measures stress the need to realize that what is normally taken as a point estimate in fact constitutes a range of values whose distribution around the mean normally remains undefined (Figure 10A). Categorical confusions of this kind in paleofaunal studies are, alas, not restricted to age estimation methods (Watson, 1978; Gautier, 1984).

CONCLUSIONS

The data here presented indicate that whereas different ageing techniques did not produce similar age profiles when applied on the same assemblage, the inference of a natural mortality, as originally postulated on account of taphonomic data (Morales & Rodríguez, 1997), seems to hold. On the other hand, the age spectra emerging after crown height measurements were applied to our sample conformed best with an attritional mortality profile characterized by a relative abundance of middle-aged specimens, as opposed to a catastrophic one as originally postulated (*Ibid*.). Notwithstanding the fact that there might well exist ultimate causes dictating such a shift from catastrophic to attritional mortality, at this point its most parsimonious explanation appears to do with strictly proximate causes, in particular the nature of the age-estimation method employed.

In analyses of animal remains from archaeological sites, age profiles are estimated with to two major goals in mind:

1) To subdivide the population into age-groups (cohorts), and
2) To estimate the age structure of that population in order to determine its mortality profile

In order to reveal environmental and cultural data that may help one infere the behaviour of the accumulating agent(s).

It now appears that, in general, and except for skeletochronology, none of the conventional age inference methods, whether qualitative or quantitative, are able to provide reliable point estimates (Dimmick & Pelton, 1994). For such reason, without an acceptable basis of inference, most relative ageing techniques are questionable, when not downright misleading, and methodological constraints inherent to the various methods bound to produce different age spectra on the same sample. Future efforts should thus focus on two aspects of the research:

1. Enlarge and refine modern inferential databases. If enough studies were to be carried out on different populations within a particular species, one would have a far more reliable idea about the range of natural variation as it concerns demography, and, consequently, a deeper understanding on how to build up a reliable system of cohorts for a particular species. Such databases would still not resolve the problems of inferring age spectra for past populations since the modern equivalents, no matter how eco-morphologically alike, may, in fact, exhibit very different ontogenetic trajectories from their extinct counterparts. This applies in particular to species with wide geographical distributions and numerous local variants as is the case, in archaeozoological studies, of the domestic mammals. Eventually, such databases would allow one to set absolute time intervals to specific cohorts (eg., Grant, 1982).
2. Combine different ageing techniques when trying to establish the mortality profile of a subfossil/fossil population. In this way, a self-corrective procedure would be introduced that would enable workers to more reliably assess the validity of a particular population's age structure, testing whether or not a certain pattern held under different circumstances.

Both recommendations make the implicit assumption that it is probably illusory to expect that an age profile from a non-living population could ever be a faithful replica of the original situation. But if precautions such as these are not taken, results not only may end up having little to do with former realities, but also, as has been from time to time the case, may mislead later workers into cascades of erroneous inferences.

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