Size frequency analysis of tooth wear in spotted hyaenas *Crocuta crocuta*

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The relative degree of attrition of the second lower premolar, in conjunction with suture coalescence and rate of closure of the pulp cavities of canine teeth, has been used to develop an age-class schedule for spotted hyaenas, consisting of seven age classes ranging from the first year to 16 years and over. A size frequency analysis of the distribution of the areas of the occlusal surface of PM_2 has been used to describe the different modes of wear, and chronological age limits are assigned to each mode by interpolation from the age-class schedule of Kruuk (1972).
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Die relatiewe mate van tandslytasie van die tweede onderste premolaar, sowel as die graad van skedelnaatversmelting en die mate van vernouing van die pulpholte van oogtande, is gebruik om 'n ouderdomsklas-skedule vir gevlekte hiënas te ontwikkel. Sewe ouderdomsklasse wat strek vanaf die eerste jaar tot 16 jaar en ouer is onderskei. 'n Groottefrekwensie-analise van die verdeling van die area van die slytasieoppervlak van PM_2 is gebruik om verskillende modules van slytasie te beskryf. Kronologiese ouderdomsgrense is toegeken aan elke module op grond van interpolasie vanaf die ouderdomsklas-skedule van Kruuk (1972).
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Age estimation of a species for which no known-age material is available, such as the spotted hyaena, can only be meaningful when based on fundamental statistical analysis of data from age-dependent criteria. Such criteria include the attrition of teeth and the relative closure of the pulp cavity of canine teeth, and these were used to develop an age-estimation technique which would conform to the statistical limitations of predictions as reviewed by Dapson (1980). Until known-age material from free-ranging spotted hyaenas can be collected, age estimation based on inferred age classes is the only option available.

Kruuk (1972) developed an age-class classification based on the relative attrition of PM_2, and assigned chronological age limits of unequal intervals to each of five age classes. The aim of the present study was to examine the validity of Kruuk's (1972) age-class schedule and to redefine each age class.

Materials and Methods

Skulls and body morphometrical data were collected from 48 hyaenas during culling operations in the Kruger National Park, South Africa. A 12 × magnification of the occlusal surface of the second lower premolar (PM_2), was drawn on cardboard with the aid of a drawing tube fitted to a stereoscopic dissecting microscope. The area of each outline drawing was taken as the mean of four consecutive readings on an electronic planimeter (AAC-400, Hayashi Denkoh Co., Ltd., Tokyo) and after being corrected for magnification, was regarded as an estimate of the area of the occlusal surface of PM_2.

The second lower premolar was measured, because the worn surface remains more easily measureable with increasing wear, and because this tooth is the best developed of the bone-crushing premolars. Irregular abrasions, in all probability owing to earlier breakage, commonly occur in the series. One tooth was almost always more worn than its ipsilateral partner, and consequently teeth on both sides of the jaw were measured. The mean was taken as an estimate of tooth attrition. Teeth with recently fractured occlusal surfaces were excluded from the sample.

Mean values for premolars were grouped into 21 size frequency classes covering the range of observations. Multimodality in the size frequency distribution was analysed according to the method of Harding (1949), as modified by Cassie (1954), following Caughley (1965).

Cumulative percentages of occlusal surface areas in the size frequency classes, were plotted on probability paper (normal-probability scale) and points of inflections in the resulting curve represented boundaries between modes (see Caughley 1965). Each mode was treated as a separate distribution to allow standard deviations to be calculated and means to be derived from the graph, following Cassie (1954). Corrections for overlap between classes were not considered necessary.

In an attempt to compare results from this analysis with those of Kruuk (1972), the same series of skulls were grouped into the four age classes of Kruuk (1972), based on a visual estimate of the amount of wear in the third lower premolar. Occlusal surface areas of individuals belonging to each of these classes, were correlated with each age class, following Dapson (1980).

A series of 10 cranial sutures was examined for coalescence and related to the classes derived from the size frequency analysis. Sutures were defined as 'closed' when coalescence has progressed along the full length of the suture, although the outline may still be visible.

The extent of closure of the canine pulp cavity was examined by X-ray. Canines of right maxillas and mandibles were extracted and mounted on clear polypropylene sheets (1,5 mm thick) using a pliable adhesive. Teeth were mounted with the plane of curvature parallel to the sheet, the lingual side facing the same direction. High definition amplification screen plates were used, with the anode to film distance of 95 cm, exposed for 1 s at 15 mA and 70 kV (Smuts, Anderson & Austin 1978). The diameter of the pulp cavity at the ventral limit of the enamel layer, and at its maximum width, were measured with a vernier calliper directly on the X-ray negative.

Results

Size frequency

Figure 1 represents an analysis of multimodality in the distribution of areas of the occlusal surfaces of PM_2, where cumulative percentage of frequency classes of identical interval are plotted on a normal-probability scale. Inflections in the line of points separate modes thereby providing a basis for the subdivision into age classes, depending on the degree of overlap between classes (see Cassie 1954). Overlap was considered negligible, and discontinuities are evident at values of 50; 60; 76; 85;7 and 97,1%.

Each group between inflections was treated as a separate distribution (see Cassie 1954), which allowed the mean of each distribution to be read off the graph as surface areas corresponding to the 50% cumulative frequency (Figure 2). Standard deviations and means for each class are presented in Table 1. Five frequency modes were identified and a sixth, representing the oldest individual, could not be defined because of only a single representative. The first mode represents hyaenas with unworn teeth, but is not representative of age class I, which is composed of individuals with deciduous premolars. Seven age classes could therefore be described.

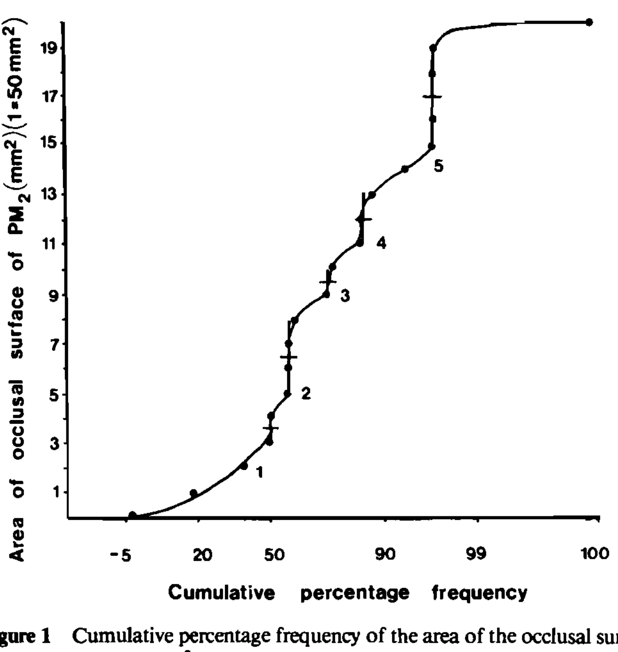

Figure 1 Cumulative percentage frequency of the area of the occlusal surface of PM_2 in 50-mm^2 classes. Bars mark inflections; numbers indicate inferred modes.

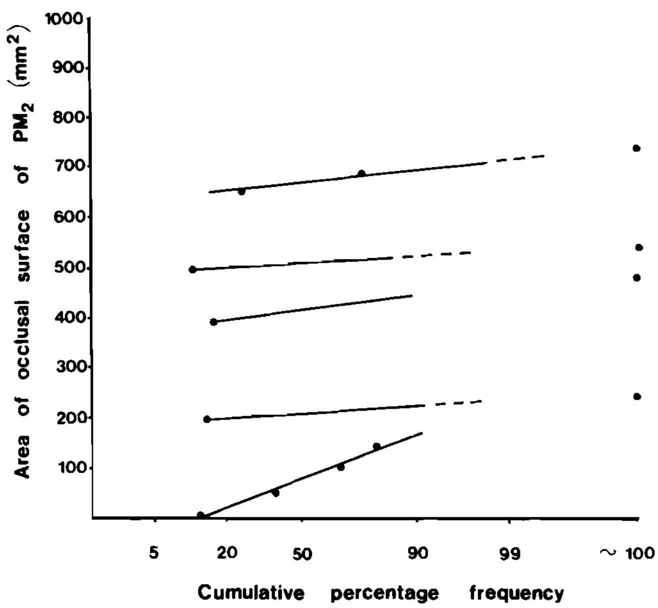

Figure 2 Inferred age classes, separated by the area of the occlusal surface of PM_2 into discrete distributions.

Table 1 Mean areas of occlusal surface (PM_2) frequency modes

	Mean area of occlusal surface PM_2 (mm^2)	SD	SE	% of total (n = 35)	n individuals per class
1	–	–	–	–	13
2	129	54	13	48	17
3	211	11	5	11	4
4	420	25	11	14	5
5	511	11	5	11	4
6	678	19	9	11	4
7	1 077	–	–	2	1

If the above classification represents equal intervals in the life-span of the hyaena, it is expected that age-dependent characters such as the coalescence of cranial sutures and the closure of the pulp cavity (Table 2), will follow a normal distribution (Laws 1968). When such an age-dependent character is plotted against age, the distribution will follow a smooth ogive, its smoothness depending on sample size. If the ogive is irregular, then the age criteria used are not sufficiently accurate, or unequal intervals between classes are demonstrated. Such an analysis has been conducted, and the incidence of coalescence of four cranial sutures in each wear class, was plotted as percentage coalesced against age. None of these resulted in a smooth ogive, or a straight line when plotting incidence against age class on probability paper (Figure 3). It can therefore be concluded that the number of years represented by each class, is not equal.

Table 2 Progressive closure of the pulp cavities of C_1^1 (minimum and maximum diameters (mm) of pulp cavities from radiograph)

Age class	N	C^1 Min.[a]	C^1 Max.[b]	C_1 Min.[a]	C_1 Max.[b]
I	27	–[c]	–[c]	–[c]	–[c]
II	15	5,9 ± 0,6	8,7 ± 0,8	5,0 ± 0,5	8,0 ± 0,8
III	9	2,7 ± 0,1	3,0 ± 0,1	2,2 ± 0,1	2,3 ± 0,1
IV	9	2,2 ± 0,3	2,6 ± 0,3	1,9 ± 0,1	2,3 ± 0,9
V	8	2,3 ± 0,1	2,6 ± 0,1	1,8 ± 0,1	2,0 ± 0,1
VI	8	2,2 ± 0,2	2,5 ± 0,3	1,8 ± 0,1	2,1 ± 0,2
VII	1	0,9	3,0	1,4	2,0

[a]Measured at ventral limit of enamel layer.
[b]Measured at maximum diameter of enamel layer.
[c]Not erupted.

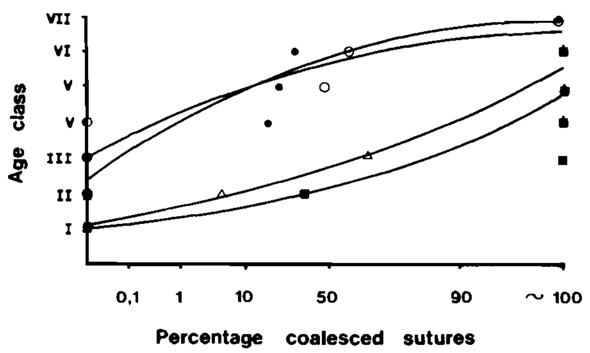

Figure 3 Incidence of fusion of four cranial sutures.

Assigning chronological ages to wear classes

The age-class classification deduced from wear classes, as described in the previous section, resulted in the identification of seven classes, where class II corresponds with wear class II of Kruuk (1972) (1 – 3 years), class III with class III (3 – 6 years), classes IV – VI with class IV (6 – 16 years) and class VII with class V (>16 years).

A linear regression analysis of mean areas of occlusal surface against the minimum age of each class, resulted in a coefficient of determination (r^2) of 1,00 indicating that all the variation in the minimum age per class, can be ascribed to changes in the area of the occlusal surface. Interpolation can therefore be validly used for projecting the chronological ages of each wear class. These are presented in Table 3. A similar analysis with maximum age as the dependent variable, also resulted in a coefficient of determination of 1,00 and chronological ages assigned to each wear class are also represented in Table 3.

Ages interpolated by means of these two ageing methods differ and it was decided to use the classification which would yield the highest coefficient of determination when the standard deviation in mean occlusal surface area of each class is regressed against the number of years in each class. This coefficient has been determined as 0,09 and 0,84 for the minimum and maximum limits per age class, as proposed by Kruuk (1972). The latter was therefore accepted and class IV therefore represents hyaenas 6 – 10 years old, class V 10 – 12 years, and class VI 12 – 16 years old (see Table 3).

Table 3 Assigning chronological ages to wear classes

n	Wear class	Age class (Kruuk 1972)	Interpolated class intervals (years) min.	Interpolated class intervals (years) max.	Mean area of occlusal surface of PM_2 (mm^2)
13	1	I (0 – 1)	0 – 1	0 – 1	–[a]
17	2	II (1 – 3)	1 – 3	1 – 3	129,0 ± 13,1
4	3	III (3 – 6)	3 – 6	3 – 6	211,0 ± 5,6
5	4		6 – 7[b]	6 – 10[b]	420,5 ± 11,3
4	5	IV (6 – 16)	7 – 10[b]	10 – 12[b]	511,0 ± 5,6
4	6		10 – 16[b]	12 – 16[b]	678,5 ± 9,8
1	7	V (> 16)	> 16	>25[c]	1077,3

[a]Not erupted.
[b]Assigned according to a linear model (min.) $y = 0{,}02x - 0{,}65$ ($r^2 = 1{,}00$) and (max.) $y = 0{,}02x + 0{,}62$ ($r^2 = 1{,}00$)
[c]Maximum longevity (Flower 1931, Crandall 1964)

Comparisons with the age-class schedule of Kruuk (1972)

In order to compare our age-class schedule with that of Kruuk (1972), occlusal surface areas of each individual were regressed against each of Kruuk's age classes. After different transformations, each followed by an analysis of residual variance, the best correlation coefficient ($r = 0{,}996$) resulted from a weighted regression analysis (Steel & Torrie 1960). However, owing to heteroscedasticity (Dapson 1980) this regression has no predictive value.

Discussion

In the absence of known-age material, the use of a size frequency analysis of a known-age-related criterion is recommended (Caughley 1965), provided that chronological age limits are assigned according to the statistical limits of predictions. Sample size is often less restrictive than array variance for the purpose of age-class definition and assignment of chronological age limits, but is often regarded as the prime cause of inaccuracy (Dapson 1980).

Chronological ages assigned to individuals according to the described method should nevertheless not be regarded as absolute, because of possible interpolation differences which would render comparisons between populations of little value. Age-related criteria, such as tooth attrition, may furthermore vary in individuals of different populations because of differences in the diet (Spinage 1973). Different diets are unlikely to affect attrition of teeth as much in carnivores as in herbivores, and the diets of hyaenas in the Kruger National Park and in Kruuk's (1972) study area were probably similar, at least as far as dietary influences on the rate of tooth attrition are concerned.

Measuring of the occlusal surface area, although tedious, is accurate and can be easily standardized. Possible sources of error are teeth with fractured occlusal surfaces causing accelerated wear in the opposite half of the jaw. Development of other age-related characters examined correspond well with the age classes defined using tooth attrition. Unfortunately, only four out of a series of 10 sutures showed progressive coalescence over such periods that would allow sufficient discrimination between age classes.

The rate of closure of the pulp cavity, although not sufficiently distinct to allow for discrimination between older age classes, was nevertheless useful as a discriminant parameter for the younger classes. It was subsequently discovered that teeth need not be extracted, but could be X-rayed intact, with the same degree of definition as when removed (anode – film distance 85 cm, exposure 60 s; 15 mA; 3,5 kV).

Relative growth, as reflected by body mass, body measurements and cranial measurements, as well as incremental cementum layers, were avoided as indicators of age, because of the many inherent sources of variance associated with these parameters. Body mass depends on the fullness of the stomach, body measurements are subject to errors in measurement, while cranial growth reaches asymptotic levels at an early stage. Annuli in the teeth of spotted hyaenas provide only inconclusive evidence as to the age of the individual, because of an irregular pattern of formation. The use of relative attrition of teeth is therefore recommended, in the absence of other reliable age criteria and known-age material. A further advantage of the technique described is that the age of live but immobilized individuals could possibly be estimated by the use of tooth impressions. This approach, however, still has to be tested under field conditions.

Acknowledgements

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