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Molar wear rates in ruminants: a new approach

N. Solounias, M. Fortelius & P. Freeman

Solounias, N., Department of Anatomy, New York College of Osteopathic Medicine, New York Institute of Technology, Old Westbury, NY 11568, U.S.A.
Fortelius, M., Division of Palaeontology, Finnish Museum of Natural History, P.O. Box 11, FIN-00014 University of Helsinki, Finland
Freeman, P., Department of Anthropology, the Graduate School of the City University of New York, NY 10036, U.S.A.

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Molar wear rates were estimated for nine ruminant species by using least-squares regression of height on age estimated from counts of cementum annuli. The relationships of molar wear rate, body mass, longevity, and new estimates of dental durability were investigated. Browsers, mixed feeders, and grazers had significantly different wear rates, but the pattern of rates was exaggerated by the body size distribution of the species examined. Height estimates divided by wear rate provide estimates of dental durability expressed in time units, and thus bypasses scaling problems. Two such durability estimates were calculated: one based on the y-intercepts of the regression equations and the other on the heights of the lower third molars. Dental durability plotted against known longevity revealed patterns among the species which can be used to evaluate the species in terms of diet and proportions of the molar row. The roe deer (*Capreolus capreolus*, a browser) has more durable molars than would be expected from its longevity and diet. The grazers have less durable first and second molars than expected, but this is compensated for by their highly durable third molars. The mixed feeders appear to have an overall dental durability in proportion to longevity. Wear rate and durability offer simple but powerful tools to estimate and investigate longevity and other parameters related to life history when longevity data are not available. Wear rate and durability seem to be the only methods presently available that is capable of generating longevity information for extinct species.

1. Introduction

Increased relative tooth height, or hypsodonty, is arguably the most common evolutionary phenomenon observed in herbivorous mammals. That hypsodonty is a response to increased dental wear is beyond doubt, but beyond this there is little agreement as to its causes and implications. Traditionally hypsodonty has been largely equated with feeding on grasses (grazing), or to a combination of grazing and increased body size (Gregory 1951, Osborn 1910, Romer 1966, Simpson 1951). Van Valen (1960: 253) constructed a "functional" index of hypsodonty, which broadened the theoretical scope of the discussion and still forms a a good conceptual basis for understanding dental durability (see also Janis & Fortelius 1988). It has proved difficult, however, to come to grips with hypsodonty and dental durability in general, and especially to analyze these phenomena in quantitative terms. The main reason for this difficulty is that the influence of diet has been difficult to separate from the influences of factors relating to body size and life span. In this paper we propose that analysis of molar wear rates presents a means of overcoming several of these difficulties.

Fortelius (1981, 1982, 1985) argued that occlusal morphology rather than crown height should be used to identify grazers among fossil species. Janis (1988) compiled and reviewed data on ungulate diets in relation to dental morphology and especially hypsodonty. One of her main conclusions was that tooth volume is better correlated with body mass than is tooth height, and that traditional measures of hypsodonty capture the dental durability of mammals inadequately. General comparisons involving species with dentitions showing different dimentions should ideally be based on several different estimates. Using only the highest (or worse, the lowest) tooth will necessarily distort the picture. According to Janis (1988) and Webb (1983), the tooth volume required by an ungulate is related by the lifetime food requirements modified by food abrasiveness.

A simple measure of dental wear is the decrease of crown height over time. Figure 1 shows the decrease in crown height for the African buffalo (*Syncerus caffer*). We refer to this as wear rate, irrespective of whether it is observed as a long-term cumulative effect (millimeters/year) or directly as "microwear" (micrometers/day). Wear rate in this sense is a useful parameter because it permits direct comparison between the short-term effects of wear and its long-term consequences in terms of dental durability, and therefore longevity is limited by the teeth (Flower 1931, Laws 1968). Wear rate also establishes a link between relative and absolute age determination — a fact of considerable importance to population studies and conservation biology, for example. It also has largely unexplored applications in paleoecology as a promising handle on longevity and related life-history parameters.

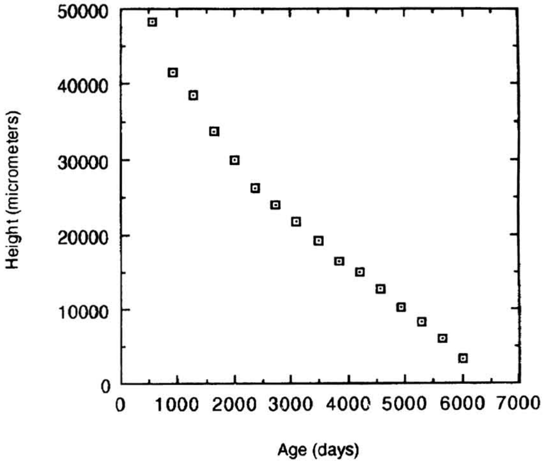

Fig. 1. Height of m1 of *Syncerus caffer* regressed on age estimated from counts of cementum annuli of the same tooth. The line is the least squares regression line. The slope gives an estimate of wear rate, the y-intercept of unworn crown height and the x-intercept of dental durability. The sigmoid distribution of data points suggest faster wear in young and old than in middle aged individuals. Data from Taylor (1988).

Previous work on wear rate in ungulates is poor. We only know of Reher and Frison (1980) who reported a general rate of tooth wear for the plains bison (*Bison bison bison*) and of Haynes (1984) who calculated the rate of tooth wear for wood bison (*Bison bison athabascae*). More studies show wear rates in various plots which are usually of tooth height against longevity or age classes, but none report a tooth wear rate (e.g. Attwell 1980, Grimsdell 1973, Haynes 1984, Severinghaus 1949). From such studies, we realized that some useful data on wear rates could be obtained. For this preliminary investigation we simply used the data that was already available in the literature, or that could easily be augmented.

Tooth microwear analysis has become an extensive method of comparison of specimens and species (reviewed by Teaford 1988). The only tooth microwear work on ruminants had an emphasis on the dietary determination of extinct species (e.g. Solounias & Moelleken 1992a, b, Solounias & Hayek 1993).

The analysis of hypsodonty in relation to food choice has been hampered by this lack of data on wear rates, but also by faulty understanding of various scaling effects. Until recently, received (and universally accepted) wisdom on this subject stated that large mammals will be more hypsodont than otherwise similar small mammals, simply because of their longer life span (e.g. Huxley 1953 p. 58). This argument is now known to be theoretically unsound, and empirical data lend strong support to the isometric scaling of tooth size predicted on theoretical grounds (Fortelius 1985, 1988, 1990a, b). There is also good evidence that dental wear scales isometrically, i.e., that wear rate is proportional to tooth size (or mouth size or body size, which are all roughly isometric) rather than a simple function of food properties (Fortelius 1987). One result of this is that dental morphology is almost entirely independent of body size: morphologically similar teeth are, for example, found in chevrotains and giraffes, in hyraxes and rhinoceroses, or in mice and mastodons. The reasons for the isometric scaling of dental wear are not currently understood, but the empirical evidence is overwhelming. Together with the known isometry of tooth size in general it means that scaling effects can be easily handled in a discussion of wear rates in mammals of different size.

Dental wear, eruption, and subsequent development are commonly used to determine the age of individuals whose age is not otherwise known. The relative merits of various methods have been debated (e.g. Habermehl 1985, Klevezal & Kleinenberg 1967, Morris 1972, 1978, Spinage 1973), but there is little doubt that the count of incremental lines in the radicular cementum constitutes one of the most reliable indicators (Morris 1972, Spinage 1973). Another good age indicator is the amount of dental wear, although this can only be applied when a standard for comparison is available (e.g. Attwell 1980, Grant 1982, Laws 1968).

A fact which seems to have escaped more widespread use is that an isolated molar potentially offers a value for both age and height. In other words, a sample of isolated teeth at various stages of wear allows direct and simple estimation of the overall wear rate for the population that they represent. Furthermore, the same regression analysis of crown height against age which gives the wear rate also gives an estimate of the unworn crown height of the tooth in question. If the height estimate (mm) is divided by the rate estimate (mm/year), the result is an estimate of dental durability expressed in years. This estimate can be directly compared with longevity, and, via transformations, with body mass and related parameters. This paper is a preliminary presentation of this insight and its methodological potential. We calculate average wear rates for several species and examine them in relation to diet, body size, longevity, and hypsodonty. Our estimates are based mostly on published reports that used different methods, and are not intended as precise comparative data. Our purpose is not to present an in-depth analysis of this limited sample that happened to be available, but to draw attention to the fact that analysis of wear rates opens up comparative possibilities which have not previously been explored.

We are aware of two articles which refer to the rate of tooth wear (Haynes 1984, Reher & Frison 1980). In both articles average wear rate was used in analysis of dietary differences between the two subspecies of Bison; plains bison and wood bison. Haynes (1984) is the only study which presents a plot of tooth height versus the age estimated from cementum annuli. We have found no reference to wear rates analyzed in relationship to dental durability, body mass, or longevity.

2. Materials and methods

The scattered publications on wear and age differ in various details, such as the tooth used, the measured height, or the preparation and counting protocol of cementum annuli. Relevant details are listed in Table 1. The differences will have a minor effect only on general comparisons such as the present study, however, and we have used the data as given for the various species. The selection of species reflects availability in the literature of cementum line counts (annuli). In most cases the lower first molar had been used for both line counts and height measurements.

We calculated molar wear rates from annuli and tooth heights. The data were all obtained from existing literature except for two species; reindeer and West African buffalo. The species included in this study (Table 1) fall into two categories. The first group consists of taxa for which data on both tooth height and annuli was available from the same individuals. They were roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), caribou (*Rangifer tarandus groenlandicus*), Grant's gazelle (Gazella granti), and American plains bison (*Bison bison bison*). Original data on 101 caribou teeth (*Rangifer tarandus groenlandicus*) were used from Canada (see Freeman, 1988 for details on this sample). All other data of the present study come from the literature (Table 1).

For the second group we supplemented published annulus counts by obtaining tooth heights from other individuals. For *Connochaetes taurinus*, Attwell (1980) gives a scoring chart of occlusal wear stages, which is a good proxy for height, and we simply measured tooth heights of individuals showing the same occlusal configuration. For *Antidorcas marsupialis* and *Ovibos moschatus* we used horn development charts given by the same source as the annuli to match crown height with age. Both species had cementum counts based on incisors, and both were excluded from the calculations involving dental durability. In the cases where we measured teeth from museum specimens, we used the height of the paracone of the upper second molar measured in buccally. These specimens were obtained from the National Museum of Natural History, Smithsonian Institution, in Washington, D.C., USA.

Microwear scar depth was measured for a browser, a mixed feeder and two grazers (Table 2). The medial enamel band of the paracone of upper second molars was molded with polyvinyl siloxane. The molds were cut from the impression side of the mold towards the jacketing. The casts were sectioned with a razor blade at right angles to the direction of scars. Thin uncoated and unmounted slices (approximately 0.5 mm thick) were examined by an electron microscope at 5 kV acceleration voltage and 500 times magnification. The depths of a representative selection of scratches were measured using the electronic measuring device of the scanning electron microscope. Features less than 0.1 micrometers in depth were ignored.

Data on body mass and longevity was obtained from the literature as cited in Table 1. Data on diet was taken from Chapman & Feldhamer (1982), Janis (1988), and Kingdon (1982). Tooth volumes, heights of m3 and indices of

Table 1. Material used and results obtained in this study.

Species	Tooth used for		Wear rate			Height estimate (y-intercept)	Height of m3 (mm)[i]	Total tooth vol. (cm^3)[i]	Index of Hypsodonty[i]	Body mass (kg)	Longevity (years)
	height	line count	*n*	yearly (mm)	daily (µm)						
Browser:											
Capreolus capreolus	m1	m1[a]	7	0.33	0.91	7.09	15.6	6.96	1.49	30.0[i]	12[f]
Mixed feeders											
Cervus elaphus	M2	m1[l]	9	0.93	2.54	15.22	21.7	17.00	2.11	153.0[i]	20[c]
Rangifer tarandus	m2	m2[r]	101	0.92	2.53	15.38	14.0	12.30	1.52	213.5[e]	15[e]
Gazella granti	m1	m1[p]	8	1.63	4.46	17.28	28.3	11.70	3.45	46.0[h]	10[p]
Antidorcas marsupialis	M2	i1[m]	4	1.41	3.87	32.84	31.8	10.30	4.89	31.0[i]	8[m]
Grazers											
Bison bison bison	m1	m1[n]	–	3.65	10.00	–	70.3	120.60	4.87	675.0[i]	22[d]
Syncerus caffer caffer	m1	m1[o]	28	2.77	7.50	47.52	47.7	77.60	3.00	754.5[k]	25[o]
Ovibos moschatus	M2	i1[g]	5	3.51	9.63	39.07	45.0	61.40	3.69	364.0[i]	20[g]
Connochaetes taurinus	M2	m1[b]	7	2.03	5.57	27.05	56.3	49.10	4.94	216.0[i]	20[b]

[a] Aitken 1975
[b] Attwell 1980
[c] Clutto-Brock et al. 1982
[d] Eisenberg 1981
[e] Freeman 1988
[f] Habermehl 1985
[g] Henrichsen & Grue 1980
[h] Hofmann 1973
[i] Janis 1988
[k] Ledger 1968
[l] Lowe 1967
[m] Rautenbach 1971
[n] Reher & Frison 1980
[o] Taylor 1988 & Grimsdell 1973
[p] Spinagde 1976
[r] present study

hypsodonty were taken from Janis (1988). Incremental lines in the cementum were counted using the method of Spinage and Brown (1988).

Wear rate was calculated by regressing tooth height on age estimated from annuli. Unweighted least-squares linear regression with age as the independent variable was used. In all cases except one, r^2 is over 0.8, and the choice of line-fitting technique is of minor importance for the value of the coefficient (= the rate estimate). The exception is *Rangifer tarandus*, where we had a large sample of limited age range (all individuals between 4 and 8 years old), giving the low value of 0.33. The least squares wear rate for this sample was 0.92 mm/year, and the reduced major axis estimate was 1.55 mm/year. Both estimates are in the range for mixed feeders obtained in this study. For consistence we used the least squares estimate, as for all the other species.

The y-intercept of the regression was used as a standardized estimate of unworn height of the molar for which the rate was calculated. To obtain an estimate of dental durability we divided the y-intercept (mm) by the wear rate (mm/year). This produced a value in years, equivalent to the x-intercept of the regression line and directly comparable to actual observed longevity. We will refer to it as "intercept durability." Another estimate of dental durability was obtained by dividing the height of unworn m3 (from Janis, 1988) with the wear rate obtained from the plots. This is denoted "m3 durability."

Significance was assessed with analysis of variance, with the non-parametric Kruskall-Wallis test as a backup since the rates do not appear to be normally distributed. For *Syncerus caffer caffer*, the two samples were averaged for all comparisons.

Tooth nomenclature: Upper teeth are designated by upper case letters (e.g. M1, M2), lower teeth with lower case letters (e.g. i1, m3).

Table 2. Microwear scar depths in four ruminants.

Species	*n*	mean±*SD*	range
Giraffa camelopardalis	5	1.282±0.281	0.90– 1.59
Ovis canadensis	13	7.738±6.688	0.60–24.90
Bison bison bison	21	4.841±9.389	0.16–44.10
Cervus canadensis	10	0.948±0.463	0.40– 1.76

3. Results

Mean wear rates differ significantly between the three dietary categories. The single browser had a wear rate of 0.33 mm/year. The mean rate for the four mixed feeders was 1.22 mm/year, while the five grazers averaged 2.93 mm/year; Table 1).

According to one-way analysis of variance, the three categories are significantly different ($F = 10.05$; $P = 0.007$). The difference between mixed feeders and grazers only was ($F = 18$; $P = 0.005$), with no overlap of their 95% confidence intervals of the rates. The corresponding Kruskall-Wallis tests gave lower significance levels, but the differences were still significant at the 95% level ($H = 6.67$; $P = 0.036$, and $H = 5.33$; $P = 0.021$, respectively).

Wear rate is strongly correlated with body mass ($r = 0.774$), mainly because the browser is small and the grazers are large. Total tooth volume is generally approximately isometric to body mass (Janis 1988) and is strongly correlated with wear rate in the present material ($r = 0.891$). Both m3 durability and intercept durability are also highly correlated with body size ($r = 0.873$ and 0.864, respectively).

The correlation between longevity and body mass was 0.839, and the least squares regression equation of longevity on body mass was $0.751(\text{body mass})^{0.29}$. The regression was calculated by using log-transformed variables, r^2 was 0.835, and the standard deviation of the exponent 0.0486. The value of the exponent is not significantly different from 0.25, which is the commonly observed value for mammals (e.g. Peters 1983). The exponent for m3 durability was 0.25, but the exponent for intercept durability was only 0.01, due to the very high durability value for the short-lived *Capreolus*. Both durability estimates were poorly correlated with maximum longevity (0.56 for m3 durability and 0.12 for intercept durability, the latter again because of *Capreolus*).

The correlation between wear rate and index of hypsodonty as given in Janis (1988) is weaker ($r = 0.625$) than between wear rate and the parameters directly related to size. Janis (1988) similarly showed a lower correlation between hypsodonty (height divided by width) and size than between size and absolute height or volume. Indeed, hypsodonty is not especially strongly

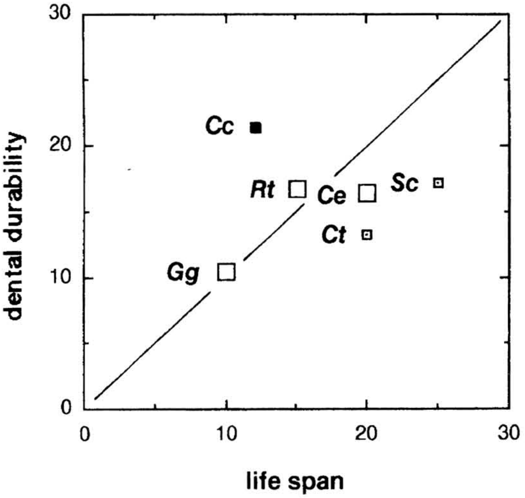

Fig. 2. Plot of dental "intercept durability" (in years) against longevity. The line denotes equal values for both variables. Note that the browsers and the grazers deviate from the line, while the mixed feeders do not.

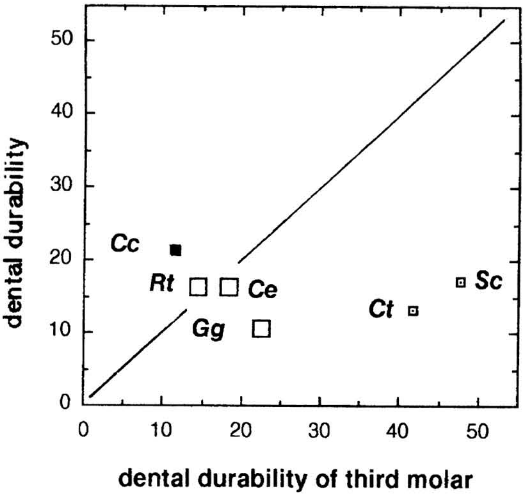

Fig. 3. Plot of "intercept durability" on "m3 durability". The pattern is similar to that in figure 2, but amplified for the grazers because of their enlarged last molars.

correlated with any of the parameters analyzed here (all coefficients < 0.8).

Plotting dental durability against maximum longevity (Fig. 2) shows a simple distribution. The mixed feeders are close to the line denoting equal magnitude of dental durability to observed longevity. The browser has a higher dental durability than would be expected from its longevity, while the opposite is true for the grazers. Grazers thus wear their teeth faster, relative to the amount of tooth available, than do the others, while the browser has "tooth to spare".

Fig. 3 shows a plot of dental durability based on the y-intercepts of the rate equations on dental durability based on the height of unworn m3 (both divided by wear rate and hence expressed in years). This shows the enlargement of the lower third molars of the grazers compared with the other groups. The mixed feeders have similar values for both estimates of durability, while the browser actually has a higher estimate based on m1 than on m3. Taken together, Figs. 2 and 3 explain the functional importance of the enlarged last molar.

A total of 49 scratches was measured, giving a total range of 0.1–44.1 micrometers (Table 2). The highest species mean (7.7 micrometers) was seen in the grazer *Ovis canadensis* (bighorn sheep), and the lowest (0.9 micrometers) in *Cervus canadensis*, a mixed feeder. Another grazer (*Bison bison bison*) had a mean of 4.8, while the browsing giraffe (*Giraffa camelopardalis*) averaged 1.3. The sample is too small for detailed comparisons but sufficient to show the approximate amount of enamel removed by individual occlusal events.

4. Discussion

All the literature data used to calculate wear rates gave very high r^2 values, while the original data used for *Rangifer tarandus* gave a much lower value. The reason for this is that all the published samples were selected for the purpose of age determination, while the reindeer material was a herd sample with a limited age range (4–8 years), emphasizing intra sample variability. The fact that the other samples were selected by no means invalidates them, however. Theoretically the best approach would be to use the means of age classes from a large random sample as a basis for the calculations, but the second-best approach is undoubtedly to select the material for even and maximum coverage of age. The samples used in this study are probably idealized to some extent, but there is no reason to believe that they are biased. In all cases but one the wear rates were calculated by us on the basis of the data provided, not by the authors themselves.

Fig. 1 shows a plot of m1 height against an age estimate based on cementum annuli from the same tooth (*Syncerus caffer*, using data from Taylor, 1988). This is clearly a selected sample, and r^2 is very high, 0.98. The data form a line with slight deviations around 1000 and 5000 days (also found for *Caprelous capreolus*, *Cervus elaphus* and *Bison bison*), which may well reflect reality. Wear is fast at first, slows down in middle age and speeds up again towards the end. The reason might simply be that the surface area of a tooth presented is very small in the earliest wear stages, so that height decrease would be rapid at first, until a larger area is exposed. Similarly in old animals the ratio of enamel to dentine begins to decrease, which would again increase the rate of height decrease. Several other factors are probably involved, but the points to be made are, first, that the data may well reflect biological reality with considerable precision, and, secondly, that for the broad-brush comparisons of the present study it is not significant whether they do or not. Our purpose is not to present a detailed study of wear rates, but to show that wear rates can elucidate problems relating to longevity and life history.

The fact that the calculated wear rates differ significantly between the dietary groups is not in itself a particularly interesting result, since the differences are compounded by intercorrelated differences in size and longevity. The mere fact that the single browser is the smallest of the species examined and the grazers are all larger than the mixed feeders is enough to cast grave doubts on its validity. And even with a less unfortunately composed sample the same principle would apply: the dietary signal would be strongly affected by the size distribution.

When the rates are used to convert dental height to dental durability in years this problem largely disappears. A plot of intercept durability against longevity (Fig. 2), for example, shows a pattern that is easy to interpret. Since both axes are in years, a line can be drawn connecting isometric points. It is immediately seen that the mixed feeders (Grant's gazelle, reindeer and red deer) fall close to this line, while the browser (roe deer) falls well above it. Both grazers (buffalo and wildebeest), on the other hand, fall below the line. Plotting dental durability against body mass gives a similar pattern, which is not surprising given the high correlation between body mass and longevity. For intercept durability, which is based variously on first and second molars, the mixed feeders are seen to have values closely corresponding to their actual longevity. The browser appears to have a higher dental durability than it needs, while that of the grazers appears insufficient for their realized longevity. This apparent paradox is resolved when m3 durability is considered.

A plot of intercept durability on m3 durability (Fig. 3) shows a somewhat similar pattern, but the grazers are now well separated by their high m3, which increases their m3 durability relative to their intercept durability. In other words, the great emphasis on m3 seen in hypsodont ruminants is seen to have a crucial functional importance, at least for the two species included here. Without it their longevity would be severely limited by dental wear.

These relatively crude estimates derived from incompletely standardized data bring out details such as these indicates that relatively subtle differences may well prove amenable to analysis if better data is collected. This possibility is especially important with regard to extinct species, for which wear rates offer a way of approaching questions relating to longevity and life history in general. A very promising application would be to investigate the evolution of hypsodonty in relation to dental durability as calculated from wear rates in fossil populations.

Longevity is known to scale approximately as body mass to the power 0.25 for mammals in general (Peters 1983). In the present small sample, the longevity value obtained (0.29) is not significantly different. It appears probable that the value 0.25 can be used to allow approximate comparisons of longevity-related parameters between animals of different size, when longevity data are not available. For example, the difference in expected longevity between an animal the size of *Capreolus capreolus* at 30 kg and another the size of *Connochaetes taurinus* at 216 kg would be $216^{0.25} / 30^{0.25} = 1.64$ (the exponent 0.29

gives the corresponding value 1.77). The difference in observed longevity (from the literature) between *Capreolus capreolus* and *Connochaetes taurinus* is very similar: 20/12 = 1.67. In this particular case, the ratio of m3 durability values is greater than that of actual longevity values (3.68) reflecting the enlarged last molar of the grazer. In contrast, the ratio of intercept durability values between the two taxa is the opposite, with the large grazer actually showing a lower value than the small browser (0.62). The implications of this were already discussed above — the point of the example is that the two species compared might, in principle, have been ones for which no actual longevity records exist.

In principle, total dental durability would be expected to scale with body mass to the power 0.25, similarly to longevity and various other life history parameters. There is no particular reason, however, for individual estimates of (partial) dental durability to scale with this exponent, since differences in proportions of the tooth row will distort the estimates. In the present study m3 durability does indeed scale with the exponent 0.25, but intercept durability was poorly correlated with body mass and the (meaningless) value of the exponent was 0.01. The reason for the anomalous scaling of the intercept durability is that the value for the short-lived *Capreolus* is very high, as discussed above. Rather than being a methodological deficiency this suggests a considerable potential for the method. Comparative analyses of different durability estimates may offer a powerful tool for understanding the functional implications of differences in proportions of the dentition between taxa. This includes such dynamic aspects as eruption sequences and rates of eruption, which may have significant effects on results.

Another important aspect of wear rate is its influence on the microwear topography, which is commonly used to reconstruct the diet of extinct species. The results of the preliminary analysis shows that even the largest microwear features found in this sample would be obliterated by wear within a short period of time. The highest mean scratch depth, 7.7 micrometers, was seen in the grazer *Ovis canadensis*. The wear rates of the grazers included in the present study range from 5.57 to 10 micrometers per day, which means that a single day's grazing would result in almost complete turnover of the microwear surface. Even the deepest scratch encountered (44.1 micrometers) would be obliterated in a few days. Species with mean scratch depths in the one micrometer range, such as the giraffe or the elk, would probably obliterate their normal microwear signal in a matter of hours if they for some reason turned to mature grass. This problem ("the Last Supper Syndrome") has been widely recognized in principle (personal communication: A. Walker, F. Grine, C. Janis, and M. Teaford), but due to the lack of data on wear rates the extreme rapidity of turnover may not have been fully appreciated previously.

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