

A comparison of observed molar wear rates in extant herbivorous mammals

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Here we review published molar wear rates, measured in terms of tooth height loss per year (mm yr^{-1}) published on natural populations of ungulates (25 species), rodents and lagomorphs (Glires; 14 species) and macropodid marsupials (seven species). Although the data are limited, they nevertheless reveal consistent patterns, and raise new questions. Among ungulates, wear rates are uncorrelated with body mass but are positively correlated with hypsodonty. Browsers show lower wear rates than do mixed feeders or grazers. Percentage of grass in the diet shows a non-linear relationship with wear rates suggesting that levels of dietary abrasives result from a complex interaction among forages, habitat characteristics and feeding behaviours (whether or not grass itself is a significant abrasive agent). Rodents exhibit higher wear rates, and kangaroos lower wear rates, than do ungulates feeding on similar diets. Hypselodont rodents and lagomorphs show rates of molar wear an order of magnitude higher than do grazing ungulates.

Introduction

Herbivorous mammals tend to experience significant degrees of tooth wear when feeding on their natural diets, and this wear presents them with an adaptive challenge. The teeth of individuals must last long enough, before being worn to the point that they lose essential function (or even being worn completely away), for the average individual to reach maturity and to reproduce successfully. Mammals have evolved a variety of adaptations to maintain tooth function in the face of high rates of tooth wear throughout life, including thickening of enamel, increase in crown height (hypsodonty), ever-growing teeth (hypselodonty), and delayed

eruption (Janis & Fortelius 1988). The rates at which the tooth crowns of herbivorous mammals are reduced in vertical dimensions by wear under natural conditions have been the subject of a voluminous discussion in zoology and, especially, palaeontology. Macroscopic tooth wear in non-primate herbivores, and the adaptations to resist it, play a large explanatory role in studies of long-term evolutionary trends and coevolution, in interpretation of diets of extinct species, and in interpretations of palaeoenvironments and palaeoclimates (e.g., Kovalevsky 1874, Simpson 1944, 1953, Van Valen 1960, Rensberger 1973, Fortelius 1985, Janis 1988a, 1988b, 1990b, MacFadden & Cerling 1994, Solounias *et al.* 1994, Fortelius & Solounias 2000, Fortelius *et al.*

2002, Fortelius *et al.* 2006, Damuth & Janis 2011, Kaiser *et al.* 2013).

It may be surprising, then, that until recently we have had little direct knowledge of the absolute rates at which herbivore teeth wear. Wear patterns have long been of interest among researchers on primates but the absolute rates of wear have seldom been reported (but *see* Teaford & Oyen 1989). Some early work measured the rates of tooth wear in a few species of Glires (e.g., Koenigswald & Golenishev 1979). A pioneering paper by Solounias, Fortelius and Freeman (Solounias *et al.* 1994) was the first to compare field-measured wear rates of ungulates. Unfortunately, the data available to these researchers were limited to nine ruminant species. Nevertheless, Solounias *et al.* (1994) showed that rates of tooth wear do, indeed, seem to differ among species as expected from diet and tooth crown height: *Capreolus capreolus* (the roe deer, the one low-crowned, browsing species in their dataset) shows a lower absolute rate of tooth wear than the higher-crowned mixed feeders and grazers. No comparative studies of ungulate wear rates have been published since, although in a few cases papers have reported data on more than one species (e.g., Veiberg *et al.* 2007). For other extant herbivore taxa whose primary adaptive response to high wear rates is thought to be increase in crown height (non-hypselodont rodents, macropodid marsupials) little has been published.

Here we present wear-rate data for 25 ungulate species, and compare rates of wear with a diverse sample of 14 rodents and lagomorphs, and seven macropodid marsupials (kangaroos and wallabies). Although still a limited sample, there is enough information to confirm widely held assumptions as well as to show some novel patterns.

Material and methods

Tooth wear rates — ungulates

For ungulates, measures of molar wear for 25 species in natural environments were obtained from the literature. For four species, multiple observations were available for populations in

habitats with substantially different vegetation, and these were recorded separately, for a total of 30 observations (Table 1). Most papers we used were concerned with techniques for ageing skull and mandibular specimens on the basis of degree of tooth wear, and such papers often reported molar enamel crown heights for samples of known-age individuals, or for individuals whose age was estimated from other criteria (such as counts of cementum lines, or time-calibrated tooth eruption stages). Any such independent age criteria that were considered reliable by the reporting authors were accepted, and criteria differed among species. In some cases, wear could be assessed only for restricted portions of the adult lifespan, but for most species the adult age-range was well represented.

Solounias *et al.* (1994) showed that it is straightforward to calculate an average rate of tooth wear from such data. Typically, ungulate molars wear comparatively rapidly immediately after coming into occlusion. Near the end of the maximum lifespan, heavily worn teeth may have lost function or integrity, and wear rates for such aged teeth may increase or decrease noticeably. However, over the majority of the adult lifespan, molar crown heights decrease in a linear or quasi-linear fashion. For each species, we have fitted ordinary least-squares best-fit lines to the linear portions of the plots of molar crown height (mm) *versus* age (yr), and expressed the slope as an average absolute wear rate (mm yr^{-1}). Most sources presented data on a single tooth position (often, the lower first molar). Some studies (e.g., Spinage 1971, Wilson *et al.* 1984) reported wear rates for a number of tooth positions and, unsurprisingly, the observed rates for different molars, uppers and lowers, tend to be very similar within a population. Accordingly, data from any and all tooth positions were regarded as comparable, and where data from more than one tooth position were reported for a species we used the mean of the corresponding wear rates.

Tooth wear rates — Glires

Data for 14 species of rodents and lagomorphs were obtained from the literature (Tables 2 and 3). For hypselodont species, Koenigswald and

Table 1. Observed molar wear rates for ungulate mammals.

Species	Wear rate (mm yr ⁻¹)	Teeth	Percentage of grass	Mass (kg)	Wear reference
<i>Aepyceros melampus</i>	2.74	M1–3, m1–3	63	53	Spinage (1971)
<i>Alces alces</i>	0.36	M1	1	384	Ericsson and Wallin (2001)
<i>Antidorcas marsupialis</i>	1.41	M2	28	31	Rautenbach in Solounias <i>et al.</i> (1994)
<i>Antilocapra americana</i>	4.19	m1	12	50	Lubinski (2001)
<i>Bison bison</i>	3.65	m1	96	658	Reher and Frison in Solounias <i>et al.</i> (1994)
<i>Bison bison</i>	1.70	m1	22.8 ^a	658	Haynes (1984)
<i>Capra pyrenaica</i>	1.92	m3	26.5	40	Fandos <i>et al.</i> (1993)
<i>Capra pyrenaica</i>	2.48	m3	76	40	Fandos <i>et al.</i> (1993)
<i>Capreolus capreolus</i>	0.49	m1	7	30	Hewison <i>et al.</i> (1999)
<i>Capreolus capreolus</i>	0.48	m1	7	30	Hewison <i>et al.</i> (1999)
<i>Ceratotherium simum</i>	2.80	M1	99	3000	Hillman-Smith <i>et al.</i> (1986)
<i>Cervus canadensis</i>	1.68	m1	75	325	Klein <i>et al.</i> (1983)
<i>Cervus elaphus</i>	1.00	m1	34	163	Carranza <i>et al.</i> (2004)
<i>Cervus elaphus</i>	0.56	m1	17	163	Loe <i>et al.</i> (2003)
<i>Cervus elaphus</i>	0.67	m1	17	163	Loe <i>et al.</i> (2003)
<i>Cervus nippon</i>	1.00	m1	36	52	Takahashi <i>et al.</i> (1999)
<i>Connochaetes taurinus</i>	2.03	M2	96	216	Attwell in Solounias <i>et al.</i> (1994)
<i>Damaliscus korrigum</i>	3.09	m1	92	115	Mertens (1984)
<i>Equus burchelli</i>	3.10	M1	96	258	Spinage (1972)
<i>Gazella granti</i>	1.40	M1	47	67	Spinage (1976)
<i>Giraffa camelopardalis</i>	0.96	M1	1	1075	Hall-Martin (1976)
<i>Muntiacus reevesi</i>	0.87	m1	2 ^b	13	Pei and Wang (1991)
<i>Odocoileus hemionus</i>	0.43	m1–3	4	74	Robinette <i>et al.</i> (1957)
<i>Odocoileus virginianus</i>	0.53	m1–3	8	51	Severinghaus (1949)
<i>Ovibos moschatus</i>	3.51	M2	30	395	Henrichsen and Grue in Solounias <i>et al.</i> (1994)
<i>Rangifer tarandus</i>	0.84	m1	17 ^c	145	Morrison and Whitridge (1997)
<i>Sylvicapra grimmia</i>	0.59	m1–3	1	13	Wilson <i>et al.</i> (1984)
<i>Syncerus caffer</i>	2.77	m1	88	360	Taylor (1988)
<i>Taurotragus oryx</i>	0.28	m3	6 ^d	511	Jeffery and Hanks (1981)
<i>Tragelaphus angasi</i>	0.71	M1	20	91	Anderson (1986)

^a Reynolds *et al.* (1978). ^b Sheng and Lu (1980), McCullough *et al.* (2000), Zheng and Bao (2007). ^c Adamczewski *et al.* (1988), McLeman (2006). ^d Codron *et al.* (2007).

Table 2. Molar wear rates for rodents with rooted, non-growing molars.

Order	Family	Species	Wear (mm yr ⁻¹)	Diet	Reference
Rodentia	Cricetidae	<i>Geoxus valdivianus</i> *	0.31	IO	Pearson (1983)
		<i>Akodon longipillius</i>	0.37	FO	Pearson (1983)
		<i>Akodon olivaceus</i>	0.38	FO	Pearson (1983)
		<i>Chelemys macronyx</i> *	0.85	FO	Pearson (1983)
		<i>Rhabdomys pumilio</i>	0.56	FG	Henschel <i>et al.</i> (1982)
		<i>Oryzomys longicaudatus</i>	0.29	FG	Pearson (1983)
		<i>Auliscomys micropus</i>	1.16	FH	Pearson (1983)
		<i>Phyllotis darwini</i>	1.26	FH	Pearson (1975)
		<i>Clethrionomys glareolus</i>	2.60	FH	Koenigswald and Golenishev (1979)
	Arvicolidae				

Diets: IO = Insectivore/Omnivore, FO = Frugivore/Omnivore, FG = Frugivore/Granivore, FH = Frugivore/Herbivore (roughly equivalent to "Browser"). * = semifossorial species. Diets from Taylor and Green (1976), Meserve (1981), Pearson (1984), Meserve *et al.* (1988), Abt and Bock (1998), supplemented by Nowak (1991). Tooth wear for *Clethrionomys glareolus* was measured on captive individuals.

Golenishev (1979) measured marked molars in captive individuals over time. For species with rooted (i.e., non-hypsodont) molars Henschel *et al.* (1982) measured tooth crown heights of lower first molar from wild individuals of known relative age (based on previous trapping of those individuals). The values from Pearson (1975, 1983) represent the decrease in average tooth crown height among individuals of an annual cohort trapped early in the season *versus* those trapped later in the season.

Tooth wear rates — Macropodids

Data from seven species of macropodid marsupials (kangaroos and wallabies) were available (Table 4). Wear rates for *Macropus robustus* (wallaroo) and *Dendrolagus lumholtzi* (Lumholtz's

tree-kangaroo) are based on measurements of known-age or independently aged individuals. The remainder are based on the authors' measurements of wild-collected museum specimens whose age was estimated from molar eruption schedules documented for each species (Ealey 1967, Poole 1973, Inns 1982, Jackson 2003, Coombes 2005).

Other data

Data for ungulate body mass are from Janis (1988b) and literature-sourced dietary information follows Janis (1988b, 1990b, 1995) unless otherwise noted in the tables. Percentage of grass in the diet represents the average annual percentage, for adults and across sexes, compiled from multiple published sources for each species

Table 3. Molar wear rates for rodents and lagomorphs with hypselodont (ever-growing) molars. Data from Koenigswald and Golenishev (1979).

Order	Family	Species	Wear (mm yr ⁻¹)	Diet
Rodentia	Arvicolidae	<i>Dicrostonyx torquatus</i>	44.2	MB
		<i>Lagurus lagurus</i>	23.4	MB
		<i>Microtus mandarinus</i>	33.8	MG
		<i>Microtus fortis</i>	28.6	MG
Lagomorpha	Leporidae	<i>Oryctolagus cuniculus</i>	62.4	MG

Natural diets (Nowak 1991): MB = Mixed browse/graze with browse dominant, MG = Mixed browse/graze with grass dominant. Note that measurements of tooth wear for hypselodonts were made on captive individuals.

Table 4. Molar wear rates for macropodid marsupials. The fossil sample of *Macropus giganteus* is from the Pleistocene Victoria Fossil Cave, South Australia, in the South Australian Museum, Adelaide. Diets as in Table 3, and BB = browser.

Species	Wear (mm yr ⁻¹)	Teeth	Diet	Percentage of grass	Wear references	Diet references
<i>Dendrolagus lumholtzi</i>	0.25	m1	BB	0	Coombes (2005)	Coombes (2005), Martin (2005)
<i>Thylogale stigmatica</i>	0.13	m2–m3	BB	0	this paper	Jarman and Phillips (1989)
<i>Setonix brachyurus</i>	0.33	m2	MB	14	this paper	Storr (1964)
<i>Macropus agilis</i>	0.18	m2–m3	MB	16	this paper	Stirrat (2002)
<i>Macropus eugenii</i>	0.51	m2–m3	MG	60	this paper	Christensen (1980) in Symon (1986)
<i>Macropus giganteus</i>	0.43	m2–m3	MG	82	this paper	Griffiths and Barker (1966) Dawson <i>et al.</i> (2004)
<i>Macropus giganteus</i> (fossil)	0.62	m3–m3	—	—	this paper	—
<i>Macropus robustus</i>	0.56	m2–m4	MG	86	Ealey (1967), this paper	Dawson and Ellis (1979)

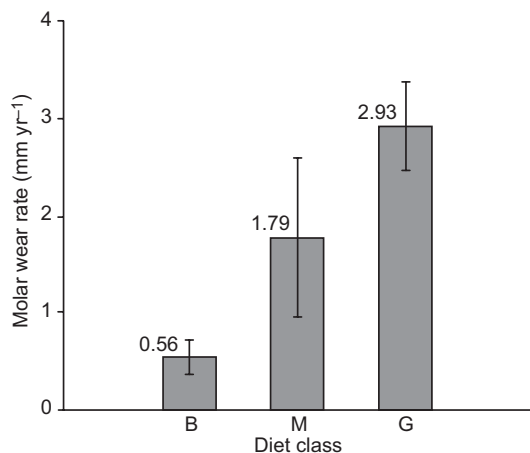


Fig. 1. Mean observed wear rate (mm yr⁻¹) \pm 2 SE for conventional ungulate diet classes. B = Browsers (\leq 10% grass in annual diet); M = Mixed feeders (between 11% and 89% grass); G = Specialized grazers (\geq 90% grass in diet). Wear rate strongly depends upon diet class (Kruskal-Wallis rank sum test: $\chi^2_2 = 17.75$, $p < 0.0001$). However, a multiple comparisons test using the *kruskalmc* function of the R package *pgirmess* (R Core Team 2012) suggests that in this dataset the means for classes M and G cannot be distinguished statistically, but both differ significantly from class B.

(Janis 1995, and unpubl. data). Although for each species values are generally consistent among studies, there is some variation presumably due to measurement error as well as real variation across populations and years. Some species are known to vary consistently and considerably among regions in the percentage of grass in their diets (e.g., *Taurotragus oryx*, *Bison bison*, *Cervus elaphus*, *Capra pyrenaica*). Generally (and especially for these four species), insofar as possible, wear rate and dietary data were matched for geographic location and habitat.

Various literature sources were used for dietary information on non-ungulates. For rodents and lagomorphs, reliable values for percentage of grass in the diet were not available for all species, so diets for these taxa are recorded only as diet classes.

Regression

Under the expectation that researchers are likely to want to predict wear rates for fossil

or unknown species, we present the equation for ordinary least-squares regression (on log-transformed variables) where a significant linear relationship exists.

Results

Ungulates

Ungulate tooth wear rates vary approximately elevenfold (Table 1), from 0.36 mm yr⁻¹ in the browser *Alces alces* (moose) to 4.1 mm yr⁻¹ in the browse-dominant mixed feeder *Antilocapra americana* (pronghorn). The conventional tripartite diet classification for ungulates (browsers, mixed feeders, and specialized grazers) is based on percentages of grass in the annual diet (Janis 1988b). For the populations in our sample the mean wear rate differs statistically among the three diet classes (Fig. 1). However, the difference is mostly due to the difference between browsers, on the one hand, and mixed feeders and grazers, on the other. Mixed feeders exhibit high variation in wear rates, which overlaps substantially with the lower end of the grazer range.

Instead of using dietary classes, we can plot tooth wear rate against percentage of grass in the diet as a continuous variable (Fig. 2). This graph shows more clearly how the data are related and reveals a striking pattern. In general, there is an apparent trend of increasing wear rate with increasing percentage of grass in the diet. However, the data overall do not seem to fit a simple linear pattern. The minimum observed wear for a given level of grass consumption appears to form a sharp, linear boundary at the bottom of the graph, along which many species cluster. In Fig. 2, we have drawn by eye this apparently linear minimum line. Above this minimum line, though, there is a considerable amount of variation; some species of a given diet may exhibit much higher rates of wear than the corresponding point on the minimum line (e.g., the pronghorn, *Antilocapra americana*, Fig. 2, number 9) and the overall distribution of points appears to be triangular or some other non-linear shape. For this reason, we do not regard a linear regression on the entire dataset to be particularly informative at this time, though the minimum line seems

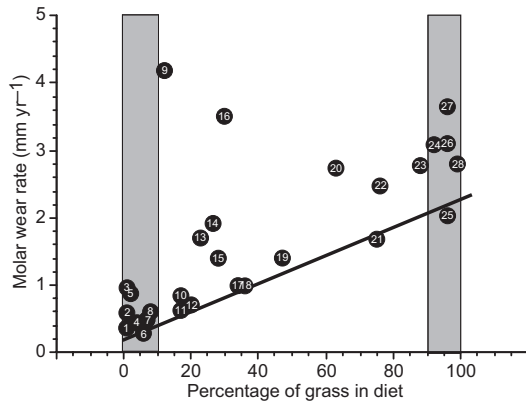


Fig. 2. Observed wear rate versus percentage of grass in the annual diet. Shaded columns indicate browsers (percentage of grass < 10%) and grazing specialists (percentage of grass > 90%). Key to species: (1) *Alces alces*; (2) *Sylvicapra grimmia*; (3) *Giraffa camelopardalis*; (4) *Odocoileus hemionus*; (5) *Muntiacus reevesi*; (6) *Taurotragus oryx*; (7) *Capreolus capreolus* (two localities, France); (8) *Odocoileus virginianus*; (9) *Antilocapra americana*; (10) *Rangifer tarandus*; (11) *Cervus elaphus* (two observations, Norway); (12) *Tragelaphus angasi*; (13) *Bison bison* (wood bison); (14) *Capra pyrenaica* (Mediterranean); (15) *Antidorcas marsupialis*; (16) *Ovibos moschatus*; (17) *Cervus elaphus* (Spain); (18) *Cervus nippon*; (19) *Gazella granti*; (20) *Aepyceros melampus*; (21) *Cervus canadensis*; (22) *Capra pyrenaica* (Alps); (23) *Syncerus caffer*; (24) *Damaliscus korrigum*; (25) *Connochaetes taurinus*; (26) *Equus burchelli*; (27) *Bison bison* (plains bison); (28) *Ceratotherium simum*.

to be telling us something. We hesitate to statistically characterize the overall distribution of points until there is more information about species that may lie in the upper region of the graph far from the minimum line.

Most species in the sample, nevertheless, do seem to lie within a region that roughly parallels the minimum line. Moreover, in those species in our sample that are known from different populations that exhibit different diets (e.g., red deer *Cervus elaphus* from Norway [11] and Spain [17], or wood bison, *Bison bison*, from Wood Buffalo National Park, Canada [13] versus plains bison [27]) the conspecific populations are related to each other on lines that roughly parallel the minimum line and the overall trend (for *Cervus elaphus*, the line joining the two populations is, essentially, the observed minimum line). In general, with respect to the minimum line and

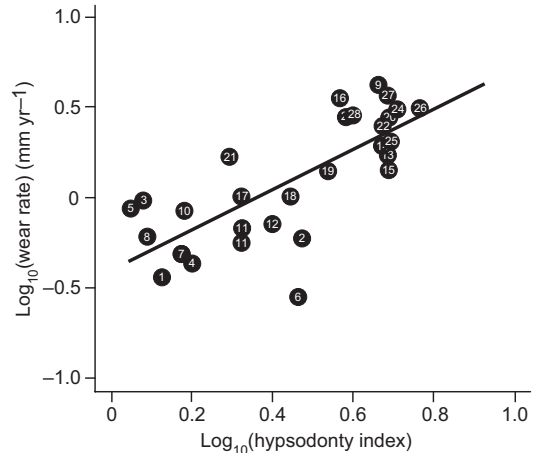


Fig. 3. Wear rate versus hypsodonty index. Numerical species identifications as in Fig. 2. Dimensionless hypsodonty index from Janis (1988b). Least-square regression (for prediction), $\log_{10}(\text{wear rate}) = 1.12 \times \log_{10}(\text{hypsodonty index}) - 0.410$ ($r^2 = 0.57$, $n = 28$, $p < 0.0001$).

the definition of browsers, mixed feeders and grazers (Janis 1988b), data in Fig. 2 suggest that mixed feeders necessarily experience tooth wear rates in excess of approximately 0.5 mm yr^{-1} , and specialized grazers necessarily experience wear rates in excess of approximately 2.0 mm yr^{-1} .

Hypsodonty is considered an evolved response to high rates of tooth wear. There is a highly significant relationship in our sample between the hypsodonty index (Janis 1988b) and the rate of tooth wear (Fig. 3). However, this relationship shows considerable variation, suggesting that a given level of hypsodonty confers a maximum rate of sustainable tooth wear, but is not inconsistent with lower rates if the circumstances permit them.

Finally, there is no relationship in our ungulate data between tooth wear rates and species average body mass, either overall or within dietary classes (Fig. 4).

Glires

Species with rooted cheek teeth in our sample (i.e., non-hypsodont species; Table 2) vary in diet from omnivory to frugivory-herbivory. The rates for omnivorous rodents, and those feeding on fruits and seeds, seem similar to those

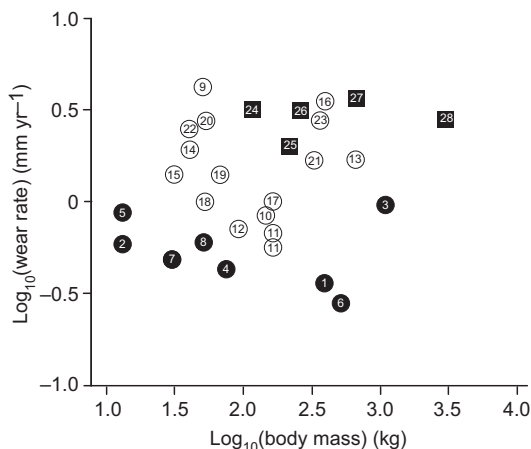


Fig. 4. Wear rate *versus* body mass. Numerical species identifications as in Fig. 2. Filled circles = browsers; empty circles = mixed feeders; filled squares = grazers. All correlations (overall, browsers, mixed feeders, grazers) are insignificant.

for browsing ungulates, but rodents that consume more leafy vegetable matter (affording the most direct dietary comparison with browsing ungulates and marsupials) show rates distinctly higher than most corresponding ungulate browsers, more similar to those for ungulate mixed feeders (Fig. 5).

Species in our sample of Glires that feed on diets primarily or substantially composed of grass have ever-growing (hypsodont) molars. Hypsodonts show extraordinarily high rates of tooth wear, an order of magnitude or more greater than those that characterize species with rooted molars; these data are not illustrated in the figures in order to save space. Although these hypsodont species were being fed a diet in captivity, it is unlikely that this diet was substantially more abrasive than their natural diet. The same study (Koenigswald & Golenishev 1979) also measured rates for the hypsodont *Clethrionomys glareolus* and found rates similar to those reported for other rodents with non-hypsodont molars (Table 3).

Macropodids

Browsing species of macropodids exhibit tooth wear rates typical for ungulate browsers, but with increasing dietary intake of grass macropo-

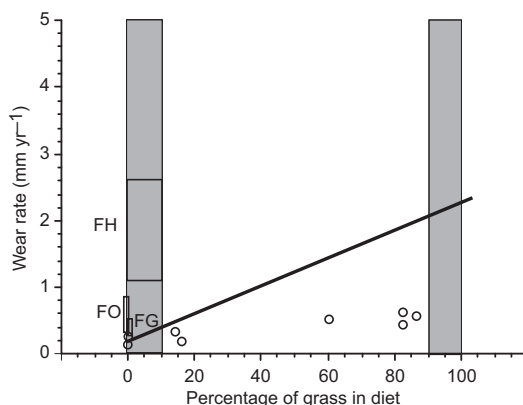


Fig. 5. Wear rates for rodents with non-hypsodont molars and for macropodid marsupials compared with those for ungulates. The conventions, axes, and scale are identical to Fig. 2., and the ungulate minimum wear line is drawn, but ungulate points from Fig. 2 are not shown. Macropodid species are plotted as circles (data from Table 4). Rodents could not be plotted as points because we do not have specific data about percentage of grass in the diet. However, the diet classes for non-hypsodont rodents in our sample correspond roughly to ungulate browsers (i.e. very low or no grass). Therefore, the range of values for a given rodent dietary class is plotted as a region in the browser region of the graph, for comparison with ungulates and marsupials of similar diet. FH = frugivore-folivore rodents; FG = frugivore-granivore rodents; FO = frugivore-omnivore rodents.

ids do not show nearly as strong an increase in wear rates as do ungulates. Wear rates for mixed feeding and grazing macropodids are as much as 4–6 times lower than those for ungulates feeding on a similar diet. Consistent with these low wear rates, macropodids also have low values of hypsodonty in comparison with ungulates of equivalent diets (Janis 1988a).

Discussion

We emphasize that the relationship between wear rate and percentage of grass in the diet is most likely *not* due to grass being inherently more abrasive than other forage (as has often been thought). Rather, increasing evidence points toward incidentally ingested soil as the primary abrasive agent for ungulate molar wear, rather than grass or its contained phytoliths (Sanson *et al.* 2007, Damuth & Janis 2011, Lucas *et al.*

2013). The relationship to percentage of dietary grass appears to derive from the fact that consuming grass obliges an animal to feed close to the ground, and to do so in an open habitat — both circumstances that maximize the exposure of the individual to incidentally ingested soil (Damuth & Janis 2011). Furthermore, specializing on a grass diet is associated in ungulates with feeding unselectively, thus decreasing the ability to choose plant parts that are free from soil. Grazing species are known to consume large quantities of soil as they feed, as does the mixed-feeding pronghorn, which also is highly hypsodont and experiences similarly high rates of tooth wear, even though it consumes relatively little grass; species exhibiting low rates of tooth wear (e.g., *Alces alces* [moose], *Odocoileus hemionus* [mule deer], *Odocoileus virginianus* [white-tailed deer]) are also found to consume relatively little soil (Damuth & Janis 2011). The fact that, particularly across the range of mixed feeders in our sample, percentage of dietary grass seems positively related to wear rate, may be because the percentage of grass in the diet largely represents the percentage of time (annually) that the animal spends feeding in a way that maximizes the intake of soil.

These observations suggest that the variation in the vertical dimension in Fig. 2 is a complex function of habitat characteristics, plant stature, and the feeding habits of particular species. Ideally, ungulates would probably all “prefer” to be feeding at the minimum wear rate that is possible, given their diet — and many species do experience wear rates near the observed ungulate minimum for their diet. However, other species necessarily encounter more abrasive diets, either because of the habitat in which they live, or because of their particular feeding habits. *Cervus elaphus* (red deer) feeds selectively in relatively closed and soil-free environments, so can live near the minimum; *Bison bison* (American bison) feeds relatively unselectively in more open and arid environments, so experiences higher tooth wear at all levels of grass consumption.

We note that the current sample of species, while illustrating some general patterns and covering what we expect are the extremes of ungulate tooth wear rates, does not yet present a com-

plete picture; some specific dietary types, such as highly frugivorous forest species and fresh-grass grazers (Janis 1988b) are not represented.

The fact that ungulate hypsodonty is not tightly correlated with wear rates is not entirely surprising. Hypsodonty represents a “wager” that tooth function on a given diet and in a given habitat will be retained until the individual has reproduced successfully, and thus to err on the side of excess is not particularly costly, but to err on the side of insufficiency is to lose substantial fitness. Thus, we might expect that for those species that experience a variety of levels of dietary abrasion, either as a species or as individuals, hypsodonty level reflects the influence of the historically highest levels of abrasion typically encountered and does not generally evolve to match closely lower levels of wear that may also be experienced in some habitats. Nevertheless there are species such as the gerenuk (*Litocranius walleri*) and dibitag (*Ammodorcas clarkei*) that have apparently secondarily evolved brachydont dentitions from more hypsodont ancestors (see Bärmann *et al.* 2013).

The lack of a statistical relationship between tooth wear rate and body mass among ungulates suggests strongly that it is the nature of the diet, especially in terms of overall abrasiveness, that determines the absolute rate of tooth wear, and that wear rate is not much affected by size-related differences in nutritional requirements, digestive physiology, or craniodental function and behaviour. Among browsers, the muntjak (*Muntiacus reevesi*; 13 kg) experiences the same rate of wear as does the giraffe (*Giraffa camelopardalis*; 1075 kg), and among grazers, the topi (*Damaliscus korrigum*; 115 kg) experiences the same wear rate as the white rhino (*Ceratotherium simum*; 3000 kg).

The relatively high tooth wear rates of hypsodont rodents feeding on leafy vegetation cannot easily be explained at our present state of knowledge. The species in the sample come from a variety of habitats, from forests to those with more open vegetation. What little information we have on soil consumption in small mammals suggests that soil as a percent of dry matter intake varies over approximately the same range (1%–7% annually) as it does in ungulates, and has a similar relationship to percentage of grass

in the diet (Garten 1980, Arthur & Gates 1988, Talmadge & Walton 1993, Beyer *et al.* 1994, Damuth & Janis 2011). The extremely high rates of tooth wear observed in hypselodont species, likewise, do not seem explicable based on differences in soil consumption or increased abrasiveness of the diet; the mixed-feeding *Lepus californicus* (black-tailed jack rabbit) has been reported to consume 6.3% soil as a percentage of dry matter intake, which is high as compared with ungulates but not out of range. Thus it appears that the somewhat elevated rates of wear in hypselodont rodents feeding partly on leaves may be the result of differences, relative to ungulates, in tooth function, enamel hardness, or feeding behaviour, but the data are so far insufficient to examine the question further. The tenfold higher wear rates seen for hypselodont species would seem to be explicable only by an increase in the susceptibility of the continuously produced enamel to wear. There are various reasons why hypselodonty is difficult to achieve in large mammals, and is only seen in a few extinct forms (*see* Janis and Fortelius 1988); however, note that in the Miocene of North America, the first hypselodont rodents appear at the same time as do the first highly hypselodont ungulates (Jardine *et al.* 2012), with the implication that rodents suffer higher levels of tooth wear than do ungulates when feeding on similar vegetation.

There are several reasons why macropodids may exhibit lower rates of tooth wear than ungulates when feeding on diets containing high percentages of grass. Firstly, mixed-feeding and grazing marsupials have basal metabolic rates that are approximately 30% lower than those of equivalent-sized placentals that feed on similar diets (McNab 1986, 1988, *see* also data compiled by Savage *et al.* 2004). These lower basal rates are reflected in lower maintenance requirements and rates of food intake; in comparison with similar sized sheep fed in captivity, the voluntary daily intake of predominantly grazing *Macropus* species is a corresponding 30%–40% lower (Forbes & Tribe 1970, Arnold 1985, Hume 1999, Munn *et al.* 2008). Since bite rates and chewing cycle times for kangaroos and similar-sized ungulates are not very different (Short 1986, Gerstner & Gerstein 2008) then the processing of less food per unit time

would imply correspondingly fewer chews and less wear on the dentition. However, metabolic considerations alone appear unable to account for all of the approximately fivefold difference between reported wear rates for grazing kangaroos and ungulates. Secondly, unlike ungulate grazers, grazing kangaroos are highly selective as to the part of the grass plant that they eat, preferring high-protein leaves and avoiding the sheath and stem (Taylor 1984, Jarman & Phillips 1989, Dawson *et al.* 2004). This behavior means that they would eat only part of the plant, and thus may be able to avoid abrasive elements such as soil attached to the plant roots (a major source of incidentally ingested soil for ungulates; *see* Damuth & Janis 2011). Kangaroos may be able to effect such selectivity due to their narrow incisor arcade (Jarman & Phillips 1989), which contrasts with the broad muzzle typical of ungulate grazers. Additionally, when feeding on many Australian grass species kangaroos may avoid ingesting soil and grit along with their food by plunging their muzzle into the middle of a stand of bunch grass rather than eating at ground level (P. Jarman pers. comm.). Finally, it is worth noting that bilophodont teeth of the kind that characterize grazing macropodids are primarily associated with low wear rates and browsing diets in marsupials, primates and ungulates. For functional reasons, bilophodont teeth cannot easily be made substantially hypselodont (Janis 1990a), so this solution to resist extremely high levels of wear is not available to such species. The instances where bilophodont teeth are used to feed on diets including large amounts of grass are relatively rare and associated with a number of specific derived morphologies (Sanson 1989, Janis 1990a, Jablonski 1994). It may be that macropodids would not have been as flexible in incorporating more abrasive diets during their later Cenozoic evolution were they not able to minimize or limit the rate of tooth wear in ways unavailable to most ungulates.

It should be noted that tooth wear among primate species has also generated a large literature (e.g., Bramblett 1969, Kay & Cant 1988, Phillips-Conroy *et al.* 2000, King *et al.* 2005, Galbany *et al.* 2011). However, because primates are brachyodont, wear-induced rates of change in height of the tooth crown have not been consid-

ered to be as informative as changes in crown morphology, and almost no data are published that are directly comparable to the wear rates reviewed here. The browsing, bilophodont *Cercoptes aethiops* fed in captivity on a “hard” diet of apples and monkey chow exhibits a tooth wear rate (0.16 mm yr^{-1}) similar to that of browsing, bilophodont macropodids (Teaford & Oyen 1989). Human wear rates are much lower, reportedly seldom exceeding 0.05 mm yr^{-1} (Teaford & Tylenda 1991).

In summary, even though absolute molar wear-rate data are currently available for only a small sample of herbivorous mammal species, the existing information is sufficient to reveal broad and consistent patterns, and to raise new questions for further investigation. Consistent with long-held assumptions, there is generally a positive relationship between molar wear rate and diets that are usually considered (and in some cases known) to be high in abrasives. Among ungulates and kangaroos, browsers generally show lower rates of wear than do mixed feeders or grazers, and among Glires species that are primarily folivorous show higher rates than do more omnivorous species. However, among ungulates wear rates are not tightly correlated with the percentage of grass in the diet, and rather seem to reflect a variety of habitat characteristics and feeding behaviours that represent different levels of dietary abrasiveness, and in particular degrees of exposure to incidental consumption of soil and grit. Moreover, rodents seem to exhibit higher wear rates, and kangaroos lower wear rates, than do ungulates feeding on similar diets. Hypselodont rodents and lagomorphs show extraordinarily high rates of molar wear, and it remains to be seen whether this is (or has been) a general feature of hypselodonty. Continued research on absolute tooth wear rates in natural environments has considerable potential to reveal selective forces involved in the evolution of dental functional morphology, ecology and palaeoecology of mammalian herbivores.

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References

- Abt, K. F. & Bock, W. F. 1998: Seasonal variations of diet composition in farmland field mice *Apodemus* spp. and bank voles *Clethrionomys glareolus*. — *Acta Theriologica* 43: 379–389.
- Adamczewski, J. Z., Gates, C. C., Soutar, B. M. & Hudson, R. J. 1988: Limiting effects of snow on seasonal habitat use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. — *Canadian Journal of Zoology* 66: 1986–1996.
- Anderson, J. L. 1986: Age determination of the Nyala *Tragelaphus angasi*. — *South African Journal of Wildlife Research* 16: 82–90.
- Arnold, G. W. 1985: Regulation of forage intake. — In: Hudson, R. J. & White, R. G. (eds.), *Bioenergetics of wild herbivores*: 81–101. CRC Press, Boca Raton, Florida.
- Arthur, W. J. & Gates, R. J. 1988: Trace element intake via soil ingestion in pronghorns and in black-tailed jackrabbits. — *Journal of Range Management* 41: 162–166.
- Bärmann, E. V., Rössner, G. E. & Wörheide, G. 2013: A revised phylogeny of Antilopini (Bovidae, Artiodactyla) using combined mitochondrial and nuclear genes. — *Molecular Phylogenetics and Evolution* 67: 484–493.
- Beyer, W. N., Connor, E. E. & Gerould, S. 1994: Estimates of soil ingestion by wildlife. — *Journal of Wildlife Management* 58: 375–382.
- Bramblett, C. A. 1969: Non-metric skeletal age changes in the Darajani baboon. — *American Journal of Physical Anthropology* 30: 161–172.
- Carranza, J., Alarcos, S., Sánchez-Prieto, C. B., Valencia, J. & Mateos, C. 2004: Disposable-soma senescence mediated by sexual selection in an ungulate. — *Nature* 432: 215–218.
- Codron, D., Codron, J., Lee-Thorpe, J. A., Sponheimer, M., de Ruiter, D., Sealy, J., Grant, R. & Fourie, N. 2007: Diets of savanna ungulates from stable isotope composition of faeces. — *Journal of Zoology (London)* 273: 21–29.
- Coombes, K. E. 2005: *The ecology and habitat utilisation of Lumholtz's tree-kangaroos, Dendrolagus lumholtzi (Marsupialia: Macropodidae), on Atherton Tablelands, far north Queensland*. — Ph.D. thesis, James Cook University, Townsville.
- Damuth, J. & Janis, C. M. 2011: On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. — *Biological Reviews* 86: 733–758.
- Dawson, T. J. & Ellis, B. A. 1979: Comparison of the diets of yellow-footed rock-wallabies and sympatric herbivores in western New South Wales. — *Australian Wildlife Research* 6: 245–254.
- Dawson, T. J., McTavish, K. J. & Ellis, B. A. 2004: Diets and

- foraging behaviour of red and eastern grey kangaroos in arid shrubland: is feeding behaviour involved in the range expansion of the eastern grey kangaroo into the arid zone? — *Australian Mammalogy* 26: 169–178.
- Ealey, E. H. M. 1967: Ecology of the Euro, *Macropus robustus* (Gould), in north western Australia. IV. Age and growth. — *CSIRO Wildlife Research* 12: 67–80.
- Ericsson, G. & Wallin, K. 2001: Age-specific moose (*Alces alces*) mortality in a predator-free environment: evidence for senescence in females. — *Ecoscience* 8: 157–163.
- Fandos, P., Orueta, J. F. & Aranda, Y. 1993: Tooth wear and its relation to kind of food: the repercussion on age criteria in *Capra pyrenaica*. — *Acta Theriologica* 38: 93–102.
- Forbes, D. K. & Tribe, D. E. 1970: The utilization of roughages by sheep and kangaroos. — *Australian Journal of Zoology* 18: 247–256.
- Fortelius, M. 1985: Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. — *Acta Zoologica Fennica* 180: 1–76.
- Fortelius, M. & Solounias, N. 2000: Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. — *American Museum Novitates* 3301: 1–36.
- Fortelius, M., Eronen, J., Jernvall, J., Liu, L., Pushkina, D., Rinne, R., Tesakov, A., Vislobokova, I., Zhang, Z. & Zhou, L. 2002: Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. — *Evolutionary Ecology Research* 4: 1005–1016.
- Fortelius, M., Eronen, J., Liu, L., Pushkina, D., Tesakov, A., Vislobokova, I. & Zhang, Z. 2006: Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 238: 219–227.
- Galbany, J., Altmann, J., Pérez-Pérez, A. & Alberts, S. C. 2011: Age and individual foraging behavior predict tooth wear in Amboseli baboons. — *American Journal of Physical Anthropology* 144: 51–59.
- Garten, C. T. 1980: Ingestion of soil by hispid cotton rats, white-footed mice, and eastern chipmunks. — *Journal of Mammalogy* 61: 136–137.
- Gerstner, G. E. & Gerstein, J. B. 2008: Chewing rate allometry among mammals. — *Journal of Mammalogy* 89: 1020–1030.
- Griffiths, M. & Barker, R. 1966: The plants eaten by sheep and by kangaroos grazing together in a paddock in south-western Queensland. — *CSIRO Wildlife Research* 11: 145–167.
- Hall-Martin, A. J. 1976: Dentition and age determination of the giraffe *Giraffa camelopardalis*. — *Journal of Zoology (London)* 180: 263–289.
- Haynes, G. 1984: Tooth wear rate in northern bison. — *Journal of Mammalogy* 65: 487–491.
- Henschel, J. R., David, J. H. M. & Jarvis, J. U. M. 1982: Age determination and age structure of a striped fieldmouse, *Rhabdomys pumilio*, population from the Cape Flats. — *South African Journal of Zoology* 17: 136–142.
- Hewison, A. J. M., Vincent, J. P., Angibault, J. M., Delorme, D., Van Laere, G. & Gaillard, J. M. 1999: Tests of estimation of age from tooth wear on roe deer of known age: variation within and among populations. — *Canadian Journal of Zoology* 77: 58–67.
- Hillman-Smith, A. K. K., Owen-Smith, N., Anderson, J. L., Hall-Martin, A. J. & Selaladi, J. P. 1986: Age estimation in the White rhinoceros (*Ceratotherium simum*). — *Journal of Zoology (London)* 210: 355–379.
- Hume, I. D. 1999: *Marsupial nutrition*. — Cambridge University Press, Cambridge.
- Inns, R. W. 1982: Age determination in the Kangaroo Island wallaby, *Macropus eugenii* (Desmarest). — *Australian Wildlife Research* 9: 213–220.
- Jablonski, N. G. 1994: Convergent evolution in the dentitions of grazing macropodine marsupials and the grass-eating cercopithecine primate *Theropithecus gelada*. — *Journal of the Royal Society of Western Australia* 77: 37–43.
- Jackson, S. M. 2003: *Australian mammals: biology and captive management*. — CSIRO Publishing, Collingwood, Victoria, Australia.
- Janis, C. M. 1988a: Why kangaroos (Marsupialia: Macropodidae) are not as hypsodont as ungulates (Eutheria). — *Australian Mammalogy* 13: 49–53.
- Janis, C. M. 1988b: An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preferences. — In: Russell, D. E., Santoro, J.-P. & Sigogneau-Russell, D. (eds.), *Teeth revisited: Proceedings of the VIIIth International Symposium on Dental Morphology, Paris, 1986*: 367–387. *Mém. Mus. Natn. Hist. Nat., Paris, series C, Paris, France*.
- Janis, C. M. 1990a: Correlation of cranial and dental variables with dietary preferences in mammals: a comparison of macropodoids and ungulates. — *Memoirs of the Queensland Museum* 28: 349–366.
- Janis, C. M. 1990b: The correlation between diet and dental wear in herbivorous mammals, and its relationship to the determination of diets of extinct species. — In: Boucot, A. J. (ed.), *Evolutionary paleobiology of behavior and coevolution*: 241–259. Elsevier, Amsterdam.
- Janis, C. M. 1995: Correlations between craniodental anatomy and feeding in ungulates: reciprocal illumination between living and fossil taxa. — In: Thomason, J. J. (ed.), *Functional morphology in vertebrate paleontology*: 76–98. Cambridge Univ. Press, Cambridge, UK and New York.
- Janis, C. M. & Fortelius, M. 1988: On the means whereby mammals achieve increased functional durability of their dentitions with special reference to limiting factors. — *Biological Reviews* 63: 197–230.
- Jardine, P. E., Janis, C. M., Sahney, S. & Benton, M. J. 2012: Grit not grass: concordant patterns of early origin of hypsodonty in Great Plains ungulates and Glires. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 365–366: 1–10.
- Jarman, P. J. & Phillips, C. M. 1989: Diets in a community of macropod species. — In: Grigg, G., Jarman, J. & Hume, I. (eds.), *Kangaroos, wallabies and rat-kangaroos*: 143–149. Surrey, Beatty & Sons, Chipping Norton, NSW, Australia.
- Jeffery, R. C. V. & Hanks, J. 1981: Age determination of eland *Taurotragus oryx* (Pallas, 1766) in the Natal Highveld. — *South African Journal of Zoology* 16: 113–122.

- Kaiser, T. M., Müller, D. W. H., Fortelius, M., Schulz, E., Codron, D. & Clauss, M. 2013: Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: implications for understanding tooth wear. — *Mammal Review* 43: 34–46.
- Kay, R. F. & Cant, J. G. H. 1988: Age assessment using cementum counts and tooth wear in a free-ranging population of *Macaca mulatta*. — *American Journal of Primatology* 15: 1–15.
- King, S. J., Arrigo-Nelso, S. J., Pocheron, S. T., Semperebon, G. M., Godfrey, L. R., Wright, P. C. & Jernvall, J. 2005: Dental senescence in a long-lived primate links infant survival to rainfall. — *Proceedings of the National Academy of Science, USA* 102: 16579–16583.
- Klein, R. G., Allwarden, K. & Wolf, C. 1983: The calculation and interpretation of ungulate age profiles from dental crown heights. — In: Bailey, G. (ed.), *The hunter-gatherer economy in prehistory*: 47–57. Cambridge University Press, New York.
- Koenigswald, W. v. & Golenishev, F. N. 1979: A method for determining growth rates in continuously growing molars. — *Journal of Mammalogy* 60: 397–400.
- Kovalevsky, V. O. 1874: Monographie der Gattung *Anthrocotherium* Cuv., und Versuch einer natürlichen Classification der fossilen Huftiere. — *Palaeontographica* 22: 210–285.
- Loe, L. E., Myserud, A., Langvatn, R. & Stenseth, N. C. 2003: Decelerating and sex-dependent tooth wear in Norwegian red deer. — *Oecologia* 135: 346–353.
- Lubinski, P. M. 2001: Estimating age and season of death of pronghorn antelope (*Antilocapra americana* Ord) by means of tooth eruption and wear. — *International Journal of Osteoarchaeology* 11: 218–230.
- Lucas, P. W., Omar, R., Al-Fadah, K., Almusallam, A. S., Henry, A. G., Michael, S., Thai, L. A., Watzke, J., Strait, D. S. & Atkins, A. G. 2013: Mechanisms and causes of wear in tooth enamel: implications for hominin diets. — *Interface, Journal of the Royal Society* 10, 20120923, doi:10.1098/rsif.2012.0923.
- MacFadden, B. J. & Cerling, T. E. 1994: Fossil horses, carbon isotopes and global change. — *Trends in Ecology and Evolution* 9: 481–486.
- Martin, R. 2005: *Tree-kangaroos of Australia and New Guinea*. — Collingwood, Victoria, Australia.
- McCullough, D. R., Pei, K. C. J. & Wang, Y. 2000: Home range, activity patterns, and habitat relations of Reeves' muntjacs in Taiwan. — *Journal of Wildlife Management* 64: 430–441.
- McLeman, C. A. I. 2006: *Determining the relationships between forage use, climate and nutritional status of barren ground caribou, Rangifer tarandus groenlandicus, on Southampton Island, Nunavut, using stable isotope analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$* . — M.Sc. thesis, University of Waterloo, Ontario, Canada.
- McNab, B. K. 1986: The influence of food habits on the energetics of eutherian mammals. — *Ecological Monographs* 56: 1–19.
- McNab, B. K. 1988: Complications inherent in scaling the basal rate of metabolism in mammals. — *Quarterly Review of Biology* 63: 25–54.
- Mertens, H. 1984: Détermination de l'âge chez le topi (*Damaliscus korrigum* Ogilby) au Parc National des Virunga (Zaire). — *Mammalia* 48: 425–435.
- Meserve, P. L. 1981: Trophic relationships among small mammals in a Chilean semiarid thorn scrub community. — *Journal of Mammalogy* 62: 304–314.
- Meserve, P. L., Lang, B. K. & Patterson, B. D. 1988: Trophic relationships of small mammals in a Chilean temperate rainforest. — *Journal of Mammalogy* 69: 721–730.
- Morrison, D. & Whitridge, P. 1997: Estimating the age and sex of caribou from mandibular measurements. — *Journal of Archaeological Science* 24: 1093–1106.
- Munn, A. J., Streich, W. J., Hummel, J. & Clauss, M. 2008: Modelling digestive constraints in non-ruminant and ruminant foregut-fermenting mammals. — *Comparative Biochemistry and Physiology A* 151: 78–84.
- Nowak, R. M. 1991: *Walker's mammals of the world*. — Johns Hopkins University Press, Baltimore.
- Pearson, O. P. 1975: An outbreak of mice in the coastal desert of Peru. — *Mammalia* 29: 375–386.
- Pearson, O. P. 1983: Characteristics of a mammalian fauna from forests in Patagonia, southern Argentina. — *Journal of Mammalogy* 64: 476–492.
- Pearson, O. P. 1984: Taxonomy and natural history of some fossorial rodents of Patagonia, southern Argentina. — *Journal of Zoology (London)* 202: 225–237.
- Pei, K. C. J. & Wang, Y. 1991: Tooth wear pattern in Formosan Reeves' muntjac (*Muntiacus reevesi micrurus*). — *Bulletin of the Institute of Zoology, Academia Sinica* 30: 341–344.
- Phillips-Conroy, J. E., Bergman, T. & Jolly, C. J. 2000: Quantitative assessment of occlusal wear and age estimation in Ethiopian and Tanzanian baboons. — In: Whitehead, P. F. & Jolly, C. J. (eds.), *Old world monkeys*: 321–340. Cambridge University Press, Cambridge.
- Poole, W. E. 1973: A study of breeding in grey kangaroos, *Macropus giganteus* Shaw and *Macropus fuliginosus* (Desmarest), in central New South Wales. — *Australian Journal of Zoology* 21: 183–212.
- Rensberger, J. M. 1973: An occlusion model for mastication and dental wear in herbivorous mammals. — *Journal of Paleontology* 47: 515–528.
- Reynolds, H. W., Hansen, R. M. & Peden, D. G. 1978: Diets of the Slave River lowland bison herd, Northwest Territories, Canada. — *Journal of Wildlife Management* 42: 581–590.
- Robinette, W. L., Jones, D. A., Rogers, G. & Gashwiler, J. S. 1957: Notes on tooth development and wear for Rocky Mountain mule deer. — *Journal of Wildlife Management* 21: 134–153.
- Sanson, G. D. 1989: Morphological adaptations of teeth to diets and feeding in the Macropodoidea. — In: Grigg, G., Jarman, J. & Hume, I. (eds.), *Kangaroos, wallabies and rat-kangaroos*: 151–168. Chipping Norton, NSW, Australia.
- Sanson, G. D., Kerr, S. A. & Gross, K. A. 2007: Do silica phytoliths really wear mammalian teeth? — *Journal of Archaeological Science* 34: 526–531.
- Savage, V. M., Gillooly, J. F., Woodruff, W. H., West, G. B., Allen, A. P., Enquist, B. J. & Brown, J. H. 2004: The

- predominance of quarter-power scaling in biology. — *Functional Ecology* 18: 257–282.
- Severinghaus, C. W. 1949: Tooth development and wear as criteria of age in white-tailed deer. — *Journal of Wildlife Management* 13: 195–216.
- Sheng, H. & Lu, H. 1980: Current studies on the rare Chinese black muntjac. — *Journal of Natural History* 14: 803–807.
- Short, J. 1986: The effect of pasture availability on food intake, species selection and grazing behaviour of kangaroos. — *Journal of Applied Ecology* 23: 559–571.
- Simpson, G. G. 1944: *Tempo and mode in evolution*. — Columbia University Press, New York.
- Simpson, G. G. 1953: *The major features of evolution*. — Columbia University Press, New York.
- Solounias, N., Fortelius, M. & Freeman, P. 1994: Molar wear rates in ruminants: a new approach. — *Annales Zoologici Fennici* 31: 219–227.
- Spinage, C. A. 1971: Geratodontology and horn growth of the impala (*Aepyceros melampus*). — *Journal of Zoology (London)* 164: 209–225.
- Spinage, C. A. 1972: Age estimation of zebra. — *East African Wildlife Journal* 10: 273–277.
- Spinage, C. A. 1976: Age determination of the female Grant's gazelle. — *East African Wildlife Journal* 14: 121–134.
- Stirrat, S. C. 2002: Foraging ecology of the agile wallaby (*Macropus agilis*) in the wet-dry tropics. — *CSIRO Wildlife Research* 29: 347–361.
- Storr, G. M. 1964: Studies on marsupial nutrition. IV. Diet of the quokka, *Setonix brachyurus* (Quoy & Gaimard), on Rottnest Island, Western Australia. — *Australian Journal of Biological Sciences* 17: 469–481.
- Symon, D. E. 1986: A survey of *Solanum* prickles and marsupial herbivory in Australia. — *Annals of the Missouri Botanical Garden* 73: 745–754.
- Takahashi, H., Kaji, K. & Koizumi, T. 1999: Molar wear rates in Sika deer during three population phases: increasing versus decline and post-decline phases. — *Mammal Study* 24: 17–23.
- Talmadge, S. S. & Walton, B. 1993: Food chain transfer and potential renal toxicity of mercury to small mammals at a contaminated terrestrial field site. — *Ecotoxicology* 2: 243–256.
- Taylor, R. D. 1988: Age determination of the African buffalo, *Syncerus caffer* (Sparrman) in Zimbabwe. — *African Journal of Ecology* 26: 207–220.
- Taylor, R. J. 1984: Foraging in the eastern grey kangaroo and the wallaroo. — *Journal of Animal Ecology* 53: 65–74.
- Taylor, K. D. & Green, M. G. 1976: The influence of rainfall on diet and reproduction in four African rodent species. — *Journal of Zoology (London)* 180: 367–389.
- Teaford, M. F. & Oyen, O. J. 1989: Differences in the rate of molar wear between monkeys raised on different diets. — *Journal of Dental Research* 68: 1513–1518.
- Teaford, M. F. & Tylanda, C. A. 1991: A new approach to the study of tooth wear. — *Journal of Dental Research* 204–207.
- Van Valen, L. 1960: A functional index of hypsodonty. — *Evolution* 14: 531–532.
- Veiberg, V., Loe, L. E., Mysterud, A., Solberg, E. J., Langvatn, R. & Stenseth, N. C. 2007: The ecology and evolution of tooth wear in red deer and moose. — *Oikos* 116: 1805–1818.
- Wilson, V. J., Schmidt, J. L. & Hanks, J. 1984: Age determination and body growth of the Common duiker *Sylvicapra grimmia* (Mammalia). — *Journal of Zoology (London)* 202: 283–297.
- Zheng, R.-Q. & Bao, Y.-X. 2007: Seasonal food habits of the black muntjac *Muntiacus crinifrons*. — *Acta Zoologica Sinica* 53: 201–207.