Contributions to Zoology, 83 (2) 107-117 (2014)

Tooth wear in captive rhinoceroses (*Diceros*, *Rhinoceros*, *Ceratotherium*: Perissodactyla) differs from that of free-ranging conspecifics

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Key words: Rhinoceros, mesowear, tooth wear, captivity, nutrition, browser, grazer

Abstract

Tooth wear can affect body condition, reproductive success and life expectancy. Poor dental health is frequently reported in the zoo literature, and abrasion-dominated tooth wear, which is typical for grazers, has been reported in captive browsing ruminants. The aim of this study was to test if a similar effect is evident in captive rhinoceros species. Dental casts of maxillary cheek teeth of museum specimens of captive black (*Diceros bicornis*; browser), greater one-horned (*Rhinoceros unicornis*; intermediate feeder) and white rhinoceroses (*Ceratotherium simum*; grazer) were analysed using the recently developed extended mesowear method for rhinoceroses. Captive *D. bicornis* exhibited significantly more abrasion-dominated tooth wear than their free-ranging conspecifics ($p<0.001$), whereas captive *C. simum* exhibited significantly less abrasion-dominated tooth wear, particularly in the posterior cusp of the second molar ($p=0.005$). In *R. unicornis*, fewer differences were exhibited between free-ranging and captive animals, but tooth wear was highly variable in this species. In both free-ranging and captive *D. bicornis*, anterior cusps were significantly more abrasion-dominated than posterior cusps ($p<0.05$), which indicates morphological differences between cusps that may represent functional adaptations. By contrast, tooth wear gradients between free-ranging and captive animals differed, which indicates ingesta-specific influences responsible for inter-tooth wear differences. Captive *D. bicornis* exhibited more homogenous tooth wear than their free-ranging conspecifics, which may be caused by an increase in the absolute dietary abrasiveness and a decrease in relative environmental abrasiveness compared to their free-ranging conspecifics. The opposite occurred in *C. simum*. The results of this study suggest that diets fed to captive browsers are too abrasive, which could result in the premature loss of tooth functionality, leading to reduced food acquisition and processing ability and, consequently, malnourishment.

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Introduction

Tooth wear experienced by free-ranging ungulates corresponds to feeding type. Browsers have attrition-dominated tooth wear, characterised by an occlusal relief (OR) that is high and a cusp shape (CS) that is sharp, whereas grazers have abrasion-dominated tooth wear, characterised by low OR and blunt CS (Fortelius and Solounias, 2000). To retain tooth functionality on high abrasion diets, grazers have evolved high-crowned (hypsodont) teeth, which are vertically elongated, enabling the tooth to wear for longer (Janis, 1988). Thus, browsers, which generally have low-crowned teeth, may not be adapted to high abrasion diets (Damuth and Janis, 2011). Excessive tooth wear has been found to influence body condition, reproductive success and longevity in many species (Skogland, 1988; Ozaki *et al*., 2010), which is attributed to reduced food acquisition and processing ability, leading to negative energy balance (Kojola *et al*., 1998). In captive wildlife, poor dental health is frequently reported (Martin Jurado *et al*., 2008), and abrasion-dominated tooth wear has been documented in captive browsing ruminants, such as giraffe (*Giraffa camelopardalis* Linnaeus, 1758) (Clauss *et al*., 2007). Captive browsing ruminants have a significantly shorter relative life expectancy than mixed feeders and grazers, which suggests there are problems providing appropriate food in captivity (Müller *et al*., 2011). Conversely, grazing ruminants, such as American bison (*Bison bison* Linnaeus, 1758), experience less abrasion-dominated tooth wear in captivity, and age at a slower rate (Kaiser *et al*., 2009; Lemaître *et al*., 2013). Therefore, unnatural tooth wear could be affecting captive animal health, welfare and longevity and, consequently, conservation strategies for captive ungulates.

The Rhinocerotidae, comprising all five extant rhinoceros species, are one of the most threatened families of mammals on Earth. Two monotypic genera and three species of rhinoceros are classified as Critically Endangered on the IUCN Red List, one as Vulnerable and one as Near Threatened. In addition to *in situ* conservation efforts in increasingly small and isolated habitat fragments, conservation breeding programmes in zoos, which exist for three of the five rhinoceros species, are a vital tool for ensuring their survival. Yet, differences in tooth wear between free-ranging and captive rhinoceroses have not been quantified, and their potential impact on the longevity, and hence lifetime reproductive output, is unknown.

Analyses of tooth wear, using the mesowear method, have been used extensively in dietary and habitat reconstruction (Fortelius and Solounias, 2000) and to compare the tooth wear patterns experienced by free-ranging and captive ruminants (Clauss *et al*., 2007; Kaiser *et al*., 2009). Recently, an extended mesowear method was developed by Winkler and Kaiser (2011) and adapted for rhinoceroses, facilitating the detection of inter-cusp and inter-tooth wear pattern differences (Taylor *et al*., 2013). In free-ranging black rhinoceros (*Diceros bicornis* Linnaeus, 1758; browser), the anterior cusps were consistently more abrasion-dominated than the posterior cusps, which may reflect a morphological adaptation to browse. In addition, both *D. bicornis* and the greater one-horned rhinoceros (*Rhinoceros unicornis* Linnaeus, 1758; mixed-feeder) had a significant tooth wear gradient, with teeth becoming less abrasion-dominated along the tooth row. Taylor *et al.* (2013) suggested that tooth wear gradients may develop due to relative changes in abrasiveness of the ingesta within the oral cavity; in particular, environmental (external) abrasives may affect the anterior teeth more severely before bolus formation. By contrast, high absolute amounts of ingested abrasives may override other signals, leading to homogenous tooth wear in white rhinoceros (*Ceratotherium simum* Gray, 1868; grazer). Comparing the tooth wear experienced by free-ranging and captive rhinoceroses could differentiate factors caused by morphology and ingesta-specific influences, because morphological constraints will remain consistent between the wild and captivity whereas ingesta-specific influences may vary in a systematic way. Therefore, the aim of this study was to quantify the degree of tooth wear observed in free-ranging and captive *D. bicornis*, *R. unicornis* and *C. simum* in order to establish whether different wear patterns are experienced in captivity.

Material and methods

Materials

We investigated 49 museum specimens of *Diceros bicornis*, *Rhinoceros unicornis* and *Ceratotherium simum* from 19 zoological museums and collections (Online Appendix S1). *C. simum* was treated as one species, instead of dividing it into *C. simum* and *C. cottoni* as recently suggested (Groves *et al*., 2010) due to the small sample size for this genus. Measurements on living specimens were not possible due to the invasiveness of the method. Only specimens with known origin from captivity were selected. Dental casts were produced of either the left or the right maxillary (upper) tooth row. A negative mould was made with Provil novo Light C.D. 2 fast set EN ISO 4823, type 3, light and Provil novo Putty regular set EN 24823 (Heraeus Kulzer GmbH, Hanau, Germany) polysiloxane dental moulding putty. One-to-one positive casts were produced by filling the moulds with epoxy resin Injektionsharz EP (Reckli-Chemiewerkstoff, Herne, Germany).

Mesowear scoring

The permanent second, third and fourth premolar (P2, P3 and P4) and the first and second molar (M1 and M2) were analysed using the adjusted rhinoceros mesowear method (Taylor *et al*., 2013). Occlusal relief (OR) and cusp shape (CS) were scored separately for the anterior and posterior cusp position due to the asymmetry of rhinoceros teeth. Rhinoceros-adjusted OR categories of 'high-high' (height/length ≥0.125), 'high' (<0.125-0.083), 'high-low' (<0.083-0.0417), 'low' (<0.0417>0.00) and 'flat-negative' (≤0), were used. CS were scored as 'sharp', 'round-sharp', 'round', 'round-round' or 'blunt' according to the degree of facet development. In addition, the posterior M2 was scored using the 'classical' mesowear method of Fortelius and Solounias (2000), with rhinoceros adjusted OR, for comparisons with previous studies (with OR scored as 'high' (≥0.03) or 'low' (<0.03) and CS as 'sharp', 'round' or 'blunt'). Digital callipers and a triplet hand lens (10x-18mm) were used, when required, to differentiate OR and CS.

As ontogeny can affect mesowear (Rivals *et al*., 2007), and specimen ages were unknown, the wear stage chart of Taylor *et al*. (2013) was used to ensure all specimens were in the same dental functional stage, excluding young and old specimens. Wear stage 6 was considered for *D. bicornis* and stages 6-7 for *R. unicornis* and *C. simum*. All pathological teeth were excluded.

Both mesowear methods were converted into a mesowear score for analysis. The extended mesowear OR and CS were converted into scores from 0 'high-high'/ 'sharp' up to 4 'flat-negative'/ 'blunt'. A mean of OR and CS was then calculated as the mesowear score (Taylor *et al*., 2013). 'Classical' mesowear results were converted into a combination score of 0 'high' and 'sharp', 1 'high' and 'round', 2 'low' and 'round', 3 'low' and 'sharp' and 4 'low' and 'blunt' (Kaiser *et al*., 2009).

Statistical analyses

Data from this study were compared to data on free-ranging specimens from Taylor *et al*. (2013). Species differences within each group (free-ranging or captive) were tested using Kruskal-Wallis tests on the posterior M2 for OR, CS and mesowear score.

Overall differences between free-ranging and captive specimens in each species were tested using linear mixed-effects (LME) models with fixed effects of Origin * Tooth position (Cusp position) and random effect of Individual specimen for the premolars (P2-P4) and molars (M1-M2) separately due to tooth wear gradients. Due to broken cusp and wear stage exclusions, sample sizes were unequal. Balanced subsamples were taken separately for the anterior and posterior cusp within each tooth to minimise loss of data. Totally balanced subsamples were tested, but resulted in substantial data loss (*R. unicornis* n=5) without changing the results. Random subsamples were taken using the statistical program R version 2.15.2 (R Core Team, 2012). We used restricted maximum likelihood (REML) and calculated denominator degrees of freedom using Satherthwaite's approximation. Differences between free-ranging and captive specimens for each individual cusp were tested on the full dataset using Welch's two sample *t*-tests, which does not assume equal variances and sample sizes (Ruxton, 2006).

Intra-species differences along the tooth row were tested using LME models with fixed effects of Cusp position and Tooth position (nested in Cusp position) and random effect of Individual specimen for the CS, OR and mesowear score for each species and origin using the subsample data. Tooth position differences were subsequently tested separately in the anterior and posterior cusp tooth row using one-way analyses of variance (ANOVA) and Dunnett's T3 post hoc test.

Statistical analyses were conducted in IBM® SPSS® Statistics 19 software (SPSS Inc., Chicago, IL) and R version 2.15.2 (R Core Team, 2012). The significance level was set to $p<0.05$.

Results

Species-specific wear signatures

Occlusal relief (OR) and mesowear scores in the posterior M2 differed significantly between the three species within both the free-ranging (Kruskal-Wallis: $p<0.001$) and captive animals ($p<0.01$). However, in contrast to the free-ranging animals, no significant difference was detected in cusp shape (CS) between captive *D. bicornis*, *R. unicornis* and *C. simum* in the posterior M2 (free-ranging: $p<0.001$; captive: $p=0.140$).

Tooth wear in free-ranging and captive animals

Overall, the CS, OR and mesowear scores in both premolars and molars were significantly more abrasion-dominated in captive *D. bicornis* (LME: all $p<0.001$), and significantly less-abrasion dominated in captive *C. simum* (all $p<0.05$), compared to their respective free-ranging conspecifics (Table 1). In *R. unicornis*, no differences were detected in molar CS ($p=0.134$), but overall mesowear scores of captive *R. unicornis* were more abrasion-dominated than their free-ranging conspecifics (all $p<0.05$). There was a subjective impression that captive specimens of all species had more

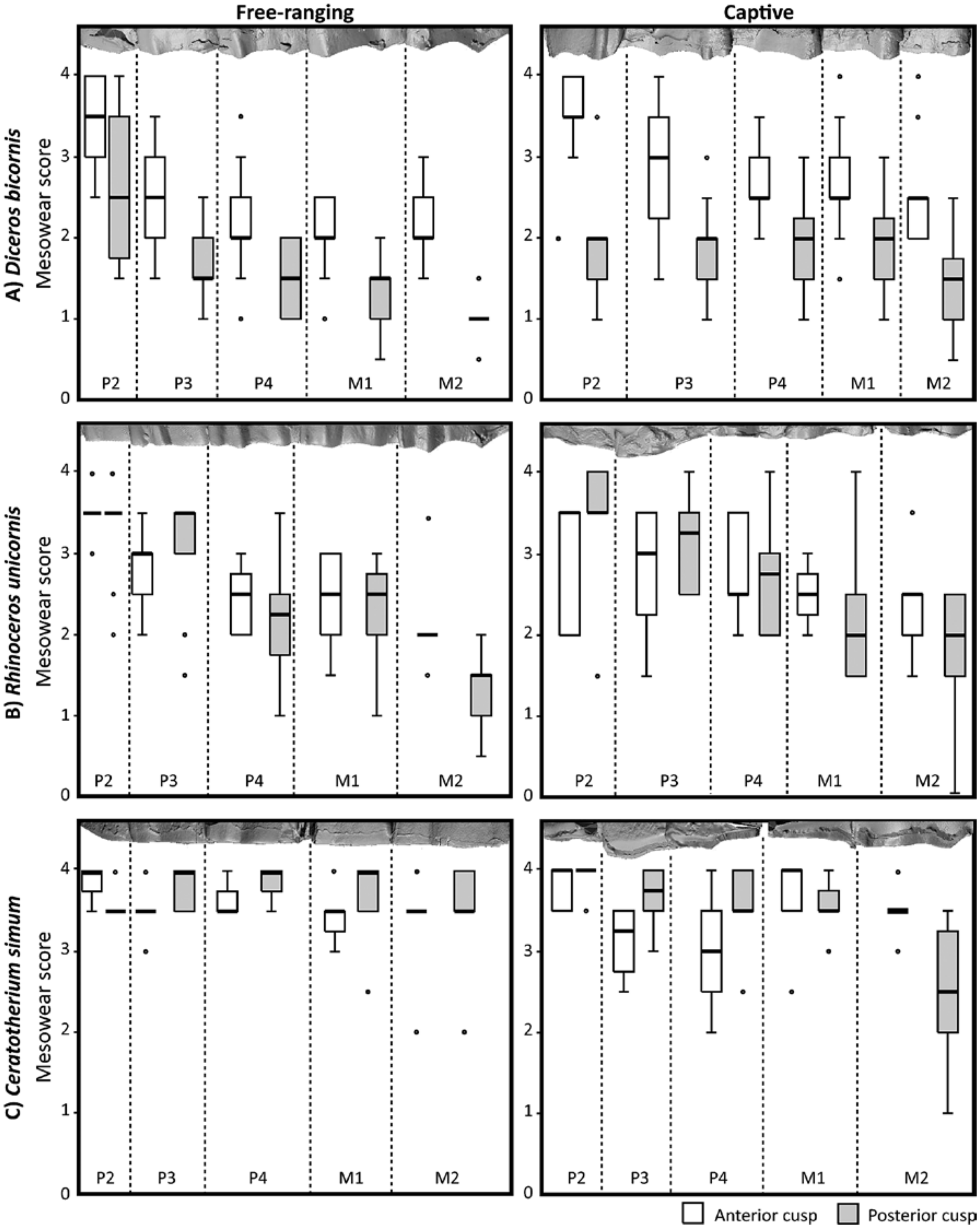

Fig. 1. Comparison of the mesowear scores for each tooth and cusp position of free-ranging and captive (a) *Diceros bicornis*, (b) *Rhinoceros unicornis* and (c) *Ceratotherium simum*. Boxplots denote the median (middle line), the upper and lower quartile (box limits), the outside interquartile range (IQR, whiskers), and outliers (defined as 1.5 times above or below the IQR). 3D scans of typical maxillary tooth rows from free-ranging and captive *D. bicornis*, *R. unicornis* and *C. simum* based on the similarity of their mesowear scores to the sample mean (Specimen identification: L-R: NMB-1021034, NMP-25963, AMNH-54455, ZMH-83585, NHM-752384, NHM-2_03). Note less even tooth wear in the captive specimens.

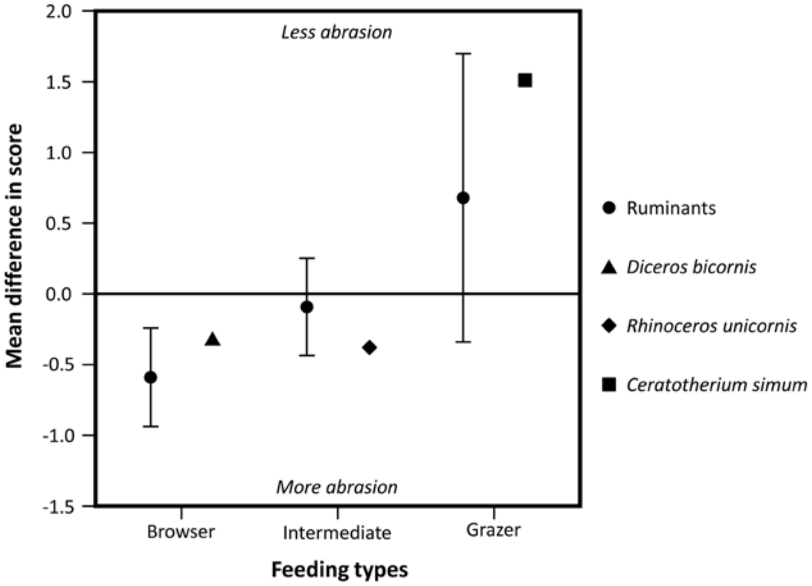

Fig. 2. Comparison of the mean score difference between captive and free-ranging ruminants and rhinoceroses (free-ranging – captive). The ruminant data is from Kaiser *et al*. (2009) and is a score difference for the whole M2 tooth position in the method of Fortelius and Solounias (2000). Rhino data, including the browser *Diceros bicornis*, mixed feeding *Rhinoceros unicornis* and grazing *Ceratotherium simum* rhinoceros, is from this study and is a score difference for the posterior cusp of M2 in the method of Fortelius and Solounias (2000) with rhinoceros adjusted OR. Error bars indicate standard deviation between ruminant species.

Table 1. Linear mixed-effects models comparing the cusp shape (CS) score, occlusal relief (OR) score and mesowear score for cusp and tooth positions, within free-ranging and captive animals, and between these groups, in *Diceros bicornis*, *Rhinoceros unicornis* and *Ceratotherium simum*. Significant differences are highlighted in **bold**.

Species	Score	Free-ranging		Captive		Origin*Tooth (Cusp)	
		Cusp	Tooth (Cusp)	Cusp	Tooth (Cusp)	P2-P4	M1-M2
Black rhino (*D. bicornis*)	CS	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	OR	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	Mesowear score	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Greater one-horned rhino (*R. unicornis*)	CS	0.729	**<0.001**	0.549	**0.007**	**0.016**	0.134
	OR	**<0.001**	**<0.001**	0.356	**<0.001**	**0.003**	**<0.001**
	Mesowear score	0.085	**<0.001**	0.918	**<0.001**	**0.005**	**<0.001**
White rhino (*C. simum*)	CS	0.503	0.213	0.625	**<0.001**	**<0.001**	**<0.001**
	OR	**0.013**	**0.014**	0.264	**<0.001**	**<0.001**	**0.021**
	Mesowear score	0.220	0.081	0.727	**<0.001**	**<0.001**	**<0.001**

uneven and atypical tooth wear (Fig. 1).

In captive *D. bicornis*, mesowear scores were significantly more abrasion-dominated in both anterior and posterior cusps of P4, M1 and M2 compared to free-ranging specimens (all $p<0.05$) (Table 2). By contrast, captive specimens had significantly less abrasion-dominated mesowear scores in the posterior cusp of P2 ($t_{21.30}=2.47$, $p=0.022$). Differences were caused by a combination of both CS and OR, with significant differences in both parameters. In captive *D. bicornis*, 57% of P2s were excluded due to advanced wear, whereas only 27% had been excluded in free-ranging specimens. Wear stage exclusions did not affect the mean mesowear score of the P2.

In *R. unicornis*, despite overall significant differences between premolars and molars, no significant differences were found between captive and free-ranging specimens at individual cusp level. Captive specimens generally had blunter CS than free-ranging specimens, but, in both groups, score variance was high. In the posterior cusp of M2, mean OR and mesowear score differences between free-ranging and captive animals were similar to *D. bicornis*.

In captive *C. simum*, CS, OR and mesowear scores

Table 2. Differences in cusp shape score, occlusal relief score and mesowear score between free-ranging and captive *Diceros bicornis*, *Rhinoceros unicornis* and *Ceratotherium simum* rhinoceroses in each tooth and cusp position for the full dataset. Populations are compared by mean ±standard deviation, the mean score difference (Score diff: free-ranging-captive) and Welch two sample *t*-tests. Significant differences are highlighted in **bold**, with values tending towards significance underlined.

			n		Cusp shape score				Occlusal relief score				Mesowear wear			
Species	Tooth and Cusp position		Free-ranging	Captive	Free-ranging	Captive	Score diff	p-value	Free-ranging	Captive	Score diff	p-value	Free-ranging	Captive	Score diff	p-value
Black rhinoceros (*D. bicornis*)	P2	A	20	9	3.7 ±0.7	3.7 ±0.7	-0.02	0.953	3.2 ±0.6	3.2 ±0.7	-0.02	0.933	3.4 ±0.5	3.4 ±0.6	-0.02	0.937
		P	20	10	2.6 ±1.1	1.9 ±1.0	0.70	0.095	2.6 ±0.8	1.8 ±0.9	0.75	**0.044**	2.6 ±0.8	1.9 ±0.7	0.73	**0.022**
	P3	A	18	12	2.5 ±0.9	2.9 ±1.0	-0.42	0.260	2.7 ±0.5	2.8 ±0.7	-0.11	0.641	2.6 ±0.6	2.9 ±0.7	-0.26	0.318
		P	18	10	1.3 ±0.8	1.9 ±0.6	-0.57	**0.036**	1.8 ±0.8	2.0 ±0.7	-0.17	0.559	1.6 ±0.4	2.0 ±0.6	-0.37	0.084
	P4	A	24	16	2.0 ±1.1	2.7 ±0.9	-0.69	**0.032**	2.4 ±0.5	2.8 ±0.4	-0.33	**0.035**	2.2 ±0.6	2.7 ±0.5	-0.51	**0.007**
		P	23	16	1.4 ±0.6	2.0 ±0.6	-0.57	**0.008**	1.7 ±0.6	2.0 ±0.7	-0.35	0.122	1.5 ±0.4	2.0 ±0.5	-0.46	**0.009**
	M1	A	22	19	2.0 ±0.7	2.6 ±0.8	-0.62	**0.016**	2.1 ±0.6	2.7 ±0.6	-0.60	**0.002**	2.0 ±0.5	2.7 ±0.6	-0.61	**<0.001**
		P	21	19	1.5 ±0.6	2.2 ±0.6	-0.68	**<0.001**	1.2 ±0.8	1.7 ±0.7	-0.50	**0.042**	1.4 ±0.5	1.9 ±0.6	-0.59	**0.002**
	M2	A	22	19	2.0 ±0.5	2.3 ±0.7	-0.26	0.171	2.2 ±0.5	2.6 ±0.6	-0.35	0.057	2.1 ±0.4	2.4 ±0.5	-0.31	**0.044**
		P	26	19	1.4 ±0.6	1.9 ±0.5	-0.56	**0.002**	0.5 ±0.6	1.0 ±0.8	-0.46	**0.044**	1.0 ±0.4	1.5 ±0.6	-0.51	**0.002**
Greater one-horned rhinoceros (*R. unicornis*)	P2	A	9	7	3.9 ±0.3	3.0 ±1.3	0.89	0.121	3.0 ±0.5	2.7 ±0.5	0.29	0.271	3.4 ±0.3	2.9 ±0.8	0.59	0.107
		P	9	7	3.6 ±0.9	3.6 ±1.1	-0.02	0.976	3.1 ±0.6	3.3 ±0.8	-0.17	0.626	3.3 ±0.7	3.4 ±0.9	-0.10	0.817
	P3	A	9	7	2.6 ±0.9	2.9 ±1.5	-0.30	0.641	2.9 ±0.3	2.7 ±0.5	0.17	0.436	2.7 ±0.5	2.8 ±0.8	-0.06	0.860
		P	9	6	3.2 ±1.1	3.7 ±0.5	-0.44	0.312	2.8 ±0.4	2.7 ±0.8	0.11	0.769	3.0 ±0.8	3.2 ±0.6	-0.17	0.644
	P4	A	7	5	2.3 ±0.5	2.8 ±1.3	-0.51	0.440	2.6 ±0.5	2.8 ±0.4	-0.23	0.441	2.4 ±0.4	2.8 ±0.7	-0.37	0.320
		P	8	6	2.5 ±0.9	3.2 ±1.0	-0.67	0.226	1.9 ±0.6	2.3 ±0.8	-0.46	0.284	2.2 ±0.8	2.8 ±0.8	-0.56	0.196
	M1	A	12	8	2.3 ±0.6	2.8 ±0.7	-0.50	0.127	2.5 ±0.7	2.3 ±0.5	0.25	0.339	2.4 ±0.6	2.5 ±0.4	-0.13	0.562
		P	11	9	2.2 ±0.9	2.2 ±1.2	-0.04	0.934	2.5 ±0.5	2.3 ±0.9	0.12	0.719	2.3 ±0.6	2.3 ±0.8	0.04	0.905
	M2	A	11	8	2.0 ±0.8	2.4 ±0.9	-0.38	0.364	2.1 ±0.3	2.4 ±0.7	-0.28	0.335	2.0 ±0.5	2.4 ±0.6	-0.33	0.224
		P	12	9	1.8 ±0.6	2.1 ±0.9	-0.36	0.331	0.8 ±0.7	1.3 ±0.9	-0.50	0.179	1.3 ±0.6	1.7 ±0.8	-0.43	0.207
White rhinoceros (*C. simum*)	P2	A	7	5	4.0 ±0.0	4.0 ±0.0	0.00	1.000	3.7 ±0.5	3.6 ±0.5	0.11	0.719	3.9 ±0.2	3.8 ±0.3	0.06	0.719
		P	7	5	4.0 ±0.0	4.0 ±0.0	0.00	1.000	3.1 ±0.4	3.8 ±0.4	-0.66	**0.029**	3.6 ±0.2	3.9 ±0.2	-0.33	**0.029**
	P3	A	9	8	3.9 ±0.3	3.4 ±0.7	0.51	0.104	3.2 ±0.4	2.9 ±0.4	0.35	0.092	3.6 ±0.3	3.1 ±0.4	0.43	**0.039**
		P	9	8	4.0 ±0.0	4.0 ±0.0	0.00	1.000	3.7 ±0.5	3.4 ±0.7	0.29	0.367	3.8 ±0.3	3.7 ±0.4	0.15	0.367
	P4	A	8	11	4.0 ±0.0	3.3 ±0.8	0.73	**0.012**	3.3 ±0.5	2.7 ±0.6	0.52	0.056	3.6 ±0.2	3.0 ±0.7	0.63	**0.013**
		P	8	10	4.0 ±0.0	3.8 ±0.6	0.20	0.343	3.8 ±0.5	3.3 ±0.5	0.45	0.062	3.9 ±0.2	3.6 ±0.4	0.33	0.063
	M1	A	7	9	3.9 ±0.4	3.9 ±0.3	-0.03	0.864	3.0 ±0.6	3.4 ±0.7	-0.44	0.194	3.4 ±0.3	3.7 ±0.5	-0.24	0.280
		P	9	8	3.6 ±0.9	3.9 ±0.4	-0.32	0.339	3.6 ±0.5	3.3 ±0.5	0.31	0.223	3.6 ±0.6	3.6 ±0.3	-0.01	0.977
	M2	A	9	11	3.8 ±0.7	4.0 ±0.0	-0.22	0.347	3.0 ±0.5	3.1 ±0.5	-0.09	0.701	3.4 ±0.5	3.5 ±0.3	-0.16	0.449
		P	9	12	3.8 ±0.7	2.6 ±1.2	1.19	**0.011**	3.3 ±0.7	2.5 ±0.7	0.83	**0.014**	3.6 ±0.6	2.5 ±0.8	1.01	**0.005**

varied, revealing both significantly more and less abrasion-dominated wear patterns than their free-ranging conspecifics. The posterior cusp of M2 was significantly sharper ($t_{17.53}=2.83$, $p=0.011$) and higher ($t_{16.91}=2.7262$, $p=0.014$) in captive than in free-ranging specimens.

In 'classical' mesowear, *D. bicornis* had a mean score difference in the posterior cusps of M2 of -0.33 (free-ranging mean =0.6±0.5; captive =0.9±0.5), *R. unicornis* -0.39 (0.8±0.4; 1.2±0.7) and *C. simum* 1.5 (3.7±1.0; 2.2±1.5) (Fig. 2). Despite a larger difference in *R. unicornis* than *D. bicornis*, no significant difference was detected in *R. unicornis* ($t_{12.04}=-1.56$, $p=0.144$), whereas significant differences were detected between free-ranging and captive *D. bicornis* ($t_{37.66}=-2.15$, $p=0.038$) and *C. simum* ($t_{18.89}=2.78$, $p=0.012$).

Cusp and tooth-specific wear signatures

In both free-ranging and captive *D. bicornis*, anterior cusps were significantly more abrasion-dominated than posterior cusps (LME: all $p<0.001$) (Table 1). By contrast, no significant differences were observed in CS and mesowear scores between cusps in free-ranging and captive *R. unicornis* and *C. simum*. Some OR cusp differences were detected in free-ranging *R. unicornis* and *C. simum*, whereas no differences were detected in captive animals.

Tooth position differences were detected in both free-ranging and captive *D. bicornis* (all $p<0.001$) and *R. unicornis* (all $p<0.01$). In contrast to free-ranging black rhinoceroses that exhibited a negative tooth wear gradient with teeth becoming less abrasion-dominated from P2-M2, captive black rhinoceroses only exhibited a significantly blunter CS in the anterior cusp of P2 ($F_{4,37}=4.91$, $p=0.002$; Dunnett's T3 post-hoc M1-M2: $p<0.01$) and a significantly higher OR in the posterior cusps of M2 ($F_{4,37}=4.97$, $p=0.001$; P3-P4: $p<0.05$) (Fig. 1). In *C. simum*, captive specimens exhibited larger differences in CS, OR and mesowear score ($p<0.001$) along the tooth row than free-ranging conspecifics (OR: $p=0.014$). Differences in captivity were predominantly due to a significantly sharper M2 (P2-M1: $p<0.05$) and higher posterior cusp of M2 (P2-M1: $p=0.009$).

Discussion

The results indicate that captive *Diceros bicornis* (browsers) exhibit more abrasion-dominated tooth wear than their free-ranging conspecifics, whereas captive *Ceratotherium simum* (grazers) exhibit less abrasion-dominated tooth wear, particularly in the posterior cusp of M2. In *Rhinoceros unicornis* (mixed-feeder), fewer differences were exhibited between the free-ranging and captive animals. Overall, differences in tooth wear pattern between the species were less pronounced in captive than in free-ranging rhinoceroses, particularly in cusp shape (CS), which did not significantly differ in the posterior cusp of M2. CS convergence indicates that the abrasiveness and/or physical properties of the diets fed in captivity are similar across all rhinoceros species. Whilst this may not be problematic for high-crowned *C. simum*, high-abrasion diets for low-crowned *D. bicornis* and also *R. unicornis* could result in the premature loss of tooth functionality, leading to reduced food processing ability and, consequently, malnourishment.

Limitations

Although a method for taking dental impressions from live rhinoceroses exists (Wucher, 1994), measurements of living specimens were not possible due to the necessity of immobilising animals for the procedure. Instead, dental casts of museum specimens were used, for which no feeding records were available. Therefore, it cannot be stated with certainty whether our findings are representative of current captive feeding practices. Individual age was indirectly controlled for in this study using functional wear stages; nevertheless, mesowear is affected by ontogeny (Rivals *et al*., 2007) and age effects cannot be excluded completely. The sample sizes of *R. unicornis* (n=11) and *C. simum* (n=15) were more limited than that of *D. bicornis* (n=23). Mesowear scoring for rhinoceroses uses different OR boundaries than ruminants; thus direct comparisons with other taxa should be limited to qualitative evaluations.

Differences between the wild and captivity

Overall, captive *D. bicornis* had more abrasion-dominated CS, OR and, consequently, more abrasion-dominated mesowear scores than their free-ranging conspecifics. Clauss *et al.* (2007) and Kaiser *et al.* (2009) suggested increased abrasion may be due to a higher intake of abrasives as plant phytoliths (silica) via grass products (such as grass hay, but also others like grain bran), and also via silica-based flow enhancers in pelleted diets. Clauss and Hatt (2006) reported two cases of excessively worn teeth in *D. bicornis* fed on grass hay. The causes of tooth wear are currently debated in the scientific literature, with some arguing that environmental abrasives have more influence (Damuth and Janis, 2011; Lucas *et al*., 2013). The high impact of external abrasives on tooth wear (Healy and Ludwig, 1965) notwithstanding, Schulz *et al*. (2013) recently found that the 3D surface textures of rabbits fed grass or lucerne distinctly differed, indicating that internal abrasives also affect dental tissue. Additionally, Rabenold and Pearson (2011) demonstrated that molar enamel thickness related to the phytolith content of the diet in 12 primate species, which suggests that increased dental durability also evolved as an adaptation to the effect of internal abrasives. Kaiser *et al*. (2009) suggested that an increase in environmental abrasives is unlikely in captivity because of increased feeding hygiene and industrial processing techniques for feeds designed to minimise soil contamination. Castell (2005) reported higher faecal acid insoluble ash (silica) values for captive *D. bicornis* (3.7±1.9% dry matter [DM], range 1.2-10.5) than reported for free-ranging *D. bicornis* (1.7±0.6 %DM; Hummel *et al*., 2011), but approaching the range measured in free-ranging *C. simum* (7.5±1.3%DM), indicating that the intake of abrasives (whether dietary, environmental, or both) is higher in captive than free-ranging browsers. Therefore, diet-specific properties may also play a significant role in tooth wear, and abrasive feeds may be causing excessive tooth wear in captive browsers.

The intrinsic toughness, physical form and chemical properties of the diet may also affect tooth wear. In domestic horses, feeding pelleted compound diets increases the vertical and decreases the lateral excursion of the chewing movement (Bonin *et al*., 2007). Taylor *et al*. (2013) suggested an increased vertical upstroke could blunt sharp cusp tips. In captive *D. bicornis*, CS was significantly blunter than in free-ranging specimens, which could also be caused by chewing compound feeds. Furthermore, chewing higher proportions of compound feeds, in parallel to similar feeding practices, could explain the lack of difference in CS scores between rhinoceros species in captivity. Imbalances of calcium (Ca), phosphorus (P) and/or vitamin D3 have also been shown to affect tooth growth and wear rates (McRoberts *et al*., 1965; Harcourt-Brown, 1996). Low serum Ca and imbalanced Ca:P ratios have been reported in captive ruminants, with enamel hypoplasia and urolithiasis in captive giraffes (Miller *et al*., 2003; Franz-Odendaal, 2004). By contrast, hypophosphatemia has been reported in captive *D. bicornis* (Dennis *et al*., 2007). The link between mineral imbalances and tooth wear should be explored further, but might not be a substantial contributing factor in captive rhinoceroses.

In *R. unicornis*, overall differences were detected between free-ranging and captive animals, but differences were not significant at individual cusp level. Taylor *et al*. (2013) suggested variability in scores in free-ranging *R. unicornis* may be due to seasonal variation in diet (53-87% grass; Pradhan *et al*., 2008). Variation in captivity likely reflects differences in feeding practices between institutions. The CS, OR and mesowear scores of free-ranging *R. unicornis* are closer to scores attained by free-ranging *D. bicornis* rather than free-ranging *C. simum*, which indicates a relatively low ingestion of environmental abrasives (Taylor *et al*., 2013). Compared to ruminant intermediate feeders studied by Kaiser *et al*. (2009), *R. unicornis* appeared to experience slightly more abrasion in captivity (Fig. 2). In addition to these scores, the generally low crown height of *R. unicornis* (Janis, 1988) indicates that high-abrasion diets may not be suitable for captive individuals of this species.

In captive *C. simum*, scores varied considerably along the tooth row, which indicates teeth are not wearing evenly. The posterior cusp of M2, the cusp typically used to interpret diet, is significantly higher and sharper than that of their free-ranging conspecifics, indicating the ingesta of captive *C. simum* is less abrasive. Kaiser *et al*. (2009) suggest captive grazers may experience less abrasion-dominated tooth wear due to reduced dietary and environmental abrasives because of the temperate climate, industrial feed processing techniques and increased feeding hygiene. In addition, the lateral excursion while chewing pelleted compound feed may be insufficient to wear the entire occlusal surface, which may facilitate the development of sharp enamel points on the edges of teeth and cause uneven tooth wear (Bonin *et al*., 2007). Elia *et al*. (2010) also found that domestic horses chewed more when fed hay (43,476 chews/day) than on pelleted diets (10,036 chews/day), which could decrease levels of tooth wear.

Cusp and tooth position differences

In both free-ranging and captive *D. bicornis*, anterior cusps were significantly more abrasion-dominated than posterior cusps. Rhino teeth are asymmetrical, with anterior cusps proportionally smaller than the posterior. Taylor *et al*. (2013) speculated that cusp differences in rhinoceroses are morphological adaptations to browse. Despite more abrasion-dominated scores, captive *D. bicornis* still exhibited significant differences between cusps, suggesting a morphological influence. This means that mesowear does not only reflect diet but also structural elements, which raises questions about the effects of tooth morphology and occlusion on the development of mesowear patterns and their functional relevance. However, anterior and posterior cusp rows were both significantly different between free-ranging and captive animals, which suggests that both cusps were also affected by ingesta-specific properties.

Free-ranging *D. bicornis* and *R. unicornis* exhibited a negative tooth wear gradient and free-ranging *C. simum* exhibited homogenous tooth wear (Taylor *et al*., 2013). By contrast, fewer differences were exhibited in tooth wear gradients between captive species. Several intrinsic (jaw biomechanics) and extrinsic factors (ingesta abrasives) might explain tooth wear gradients. Taylor *et al*. (2013) suggested tooth wear gradients may be caused by ingesta abrasiveness, because free-ranging *C. simum* consume high *absolute* amounts of ingesta abrasives, which will override other signals. The results of this study corroborate an ingesta-specific influence because the gradients differed between free-ranging and captive animals. Environmental abrasives probably affect the anterior teeth more severely before being mixed into the bolus. Captive *D. bicornis* may consume less environmental abrasives and more endogenous dietary abrasives. Thus, captive *D. bicornis* may experience less *relative* changes in abrasiveness along the tooth row and an overall increase in the *absolute* ingesta abrasiveness, leading to more homogenous tooth wear. Captive *C. simum* may experience a reduction in the *absolute* abrasiveness of ingesta compared to free-ranging conspecifics, which may lead to more pronounced *relative* changes in wear from P2-M2. The results do not negate a role of jaw biomechanics, as the OR of the posterior cusp of M2 of all captive specimens was higher than more anterior tooth positions.

In free-ranging *D. bicornis*, the P2 was significantly more abrasion-dominated than the other tooth positions, which Taylor *et al*. (2013) suggest may indicate the P2 has a role in food cropping as rhinoceroses do not have occluding incisors. By contrast, captive *D. bicornis* had homogenous tooth wear between P2-M1 in the posterior cusp tooth row. In captivity, animals are mostly fed loose hay and pelleted feeds, which may not require cropping, and may be less contaminated with environmental abrasives, such as dust adherent on browse. Therefore, food presentation, particularly the combination of reduced bite force and reduced environmental abrasives, could also affect tooth wear gradients. However, in captive *D. bicornis*, 57% of P2 teeth were excluded due to advanced wear compared to 27% in the free-ranging animals. Although age differences cannot be excluded, the P2 wear in captive specimens highlights that despite less abrasion-dominated mesowear scores, total tooth wear (volume loss) was still high (or higher) than in free-ranging specimens, which raises questions about tooth wear rate relative to mesowear pattern.

Implications

The results in rhinoceroses and ruminants (Kaiser *et al*., 2009) suggest that diets fed to captive browsers are more abrasive than their diet in the wild. Although fewer differences were exhibited in mixed-feeding *R. unicornis*, the low crown height of this species still suggests high-abrasion diets may not be suitable. Excessive tooth wear could have serious implications on captive animal health, welfare and longevity and, consequently, conservation and re-introduction strategies. In the past, captive-raised *D. bicornis* have been reintroduced into protected reservations. Releasing rhinoceroses with excessive tooth wear relative to age could to some extend jeopardise the viability of such programmes. By contrast, captive *C. simum* exhibited significantly less abrasion-dominated tooth wear than free-ranging conspecifics. Decreased tooth wear may result in prolonged tooth functionality, which may have a positive influence on longevity. However, insufficient tooth wear may lead to uneven wear and tooth pathologies, which could negatively impact on captive animal health and may contribute to other dental diseases. Dental health checks should therefore be part of routine animal health checks for rhinoceroses during any veterinary treatment. As mentioned above, Wucher (1994) describes a method of taking dental impressions from rhinoceroses, which could be used to aid in the diagnosis of tooth wear problems. To help prevent tooth wear problems, browsers and intermediate feeders should be fed on a dicot-based (browse) diet that is low in abrasives, including dicot-based pellets, and grazers should be fed on a monocot-based diet, especially grass and grass hay. Pelleted feed quantities should probably be reduced. Further research is required into the abrasiveness of the diets of captive wild animals.

Acknowledgements

We acknowledge the support provided by the American Museum of Natural History New York, Institute for Zoo and Wildlife Research Berlin, Museum National d'Histoire Naturelle Paris, National Museum Prague, National Museums Scotland Edinburgh, Naturhistorisches Museum Bern, Natural History Museum

London, Staatliches Museum für Naturkunde Stuttgart, Naturhistorisches Museum Basel, Naturhistorisches Museum Wien, Naturhistoriska Riksmuseet Stockholm, Oxford University Museum of Natural History, Phyletisches Museum Jena, Forschungsinstitut und Naturmuseum Senckenberg Frankfurt/Main, Museum für Naturkunde Berlin, Zoo Basel, Zoologisches Forschungsmuseum Alexander Koenig Bonn, Zoologisches Museum Hamburg, Zoologisches Museum Zürich and Zoologische Staatssammlung München. We thank Nelson Mascarenhas (University of Hamburg) and Olaf Dülfer (University of Bonn) for technical support, Dr Jon Bridle (University of Bristol) for his support, and Dr Amy Plowman (Whitley Wildlife Conservation Trust) and Professor Innes Cuthill (University of Bristol) for helpful comments. LT was supported by the Sir Kenneth Blaxter scholarship from the British Society of Animal Science. DM was supported by the 'Forschungskredit der Universität Zürich', loan number 55220702. This research was supported by the 'Deutsche Forschungsgemeinschaft' (DFG, German Research Foundation, KA 1525 / 8-2) and is publication no. 58 of the DFG Research Unit 771 'Function and performance enhancement in the mammalian dentition - phylogenetic and ontogenetic impact on the masticatory apparatus'. We also thank Daniela C. Kalthoff and one anonymous reviewer for their helpful comments.

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Received: 2 November 2013
Revised and accepted: 21 January 2014

Editor: V. Nijman

On-line Supplementary Information (SI)

S1. Museum and specimen information.

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Museum Abbreviation	**Museum Name**	**Specimen identification**	
		Free-ranging	**Captive**
AMNH	American Museum of Natural History New York	54454, 54455, 51854, 146718	
IZW	Institute for Zoo and Wildlife Research Berlin		371/2003, 0175, 538, 2001, 835/93
MHN	Museum National d'Histoire Naturelle Paris	A2277	1944-278, 1961-195, 1974-124, 1960-59, 1967-101, 2005-297
NHB	Naturhistorisches Museum Bern	1021034	10594, n.N.082
NHM	Natural History Museum London	1874.11.2.2, 1876.2.15.5, 19.7.15.511, 1907.2.26.1, 1948.1.28.6, 1962.7.6.1, 1962.7.6.5, 1962.7.6.6, 1967.7.6.4, 1976.9.26.6, 2.11.18.7, 1951.11.30.2, 72.12.30.1, 72.739, 84.1.22.1+2, 1967.8.31.4, 25.5.23.1, 52.12.9.1, 75.2384	1961.5.10.1
NHS	Staatliches Museum für Naturkunde Stuttgart	32018, 7564, 1218	
NMAB	Naturmuseum Augsburg		01, 02
NMB	Naturhistorisches Museum Basel	7351, C.1798	n.N.007
NMP	National Museum Prague		165, 2007, 25963, 25964, 47655, 48347, 489, 1/188, 2006, 47145
NMS	National Museums Scotland Edinburgh		200.369, 2008 unreg, 2003.5, 2008.124, 2000.33, 2004.75, 2005.129.2, 2008.127, 2009.10
NMW	Naturhistorisches Museum Wien	4279, 4291	55210
NRM	Naturhistoriska Riksmuseet Stockholm	A591324, A591596	
OUM	Oxford University Museum of Natural History	7118, 3827	
PMJ	Phyletisches Museum Jena	651	
SMF	Forschungsinstitut und Naturmuseum Senckenberg Frankfurt am Main	22660, 699, 664	15934, 40543
Zoo Basel	Zoo Basel		Zoo Basel
ZFMK	Zoologisches Forschungsmuseum Alexander Koenig Bonn		88.16
ZMB	Museum für Naturkunde Berlin	35744, 40053, 41480, 46166, 83230, 83232	
ZMH	Zoologisches Museum Hamburg	35744, 40053, 41480, 46166, 83230, 83232, 2551, 2552	8405, 9328, 8385, 10060
ZMZ	Zoologisches Museum Zürich	83226, 10806, 10927	18129, 19660, 20165, 20273
ZSSM	Zoologische Staatssammlung München	1963/160, AM416, 1912/4199, 1912/4202	2001/33