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Comparative Demography and Dietary Resource Partitioning of Two Wild Ranging Asiatic Equid Populations

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Comparative demography and dietary resource partitioning of two wild ranging Asiatic equid populations¹

E. Schulz, T.M. Kaiser, A. Stubbe, M. Stubbe, R. Samjaa, N. Batsajchan, J. Wussow

Abstract

Tooth wear signatures allow inference on the dietary traits of herbivorous ungulates. Comparing dietary regimes of taxonomically closely related populations further allows inference on habitat structure and food availability. The mesowear method of tooth wear evaluation has opened up a pathway to reconstruct subtle differences in dietary behaviour and resource partitioning based on skeletal material as the only source of information. Eighty cheek dentitions of Asian wild asses (*Equus hemionus*) from the Southern Gobi (Mongolia) and 61 dentitions of African free ranging donkeys (*Equus asinus*) from the Emirate Sharjah (United Arab Emirate) were investigated for their mesowear signatures. It is tested if sexes and age classes of individuals are different in their mesowear signatures. Cluster analyses and principal components analyses are applied in order to test hypotheses using 27 ungulate species with known diets as a reference. The wild asses from the Gobi are found to classify as typical grazers within this spectrum and have a more abrasion-dominated signature than the donkey population from the United Arab Emirates (UAE). The diet available to the latter population is thus considered to be more heterogeneous. This indicates that the donkey habitat in the UAE is a more diverse mosaic of feeding resources compared to the wild ass habitat of the Mongolian desert. In both populations there are more intraspecific differences in the diet between sexes than there are interspecific differences between the two African zebra species *E. burchellii* and *E. grevyi*. The dietary signal is further interpreted as to reflect the social structure of the animals as associated with specific environmental conditions. Between the two sexes of Asian wild asses and UAE donkeys, one would expect a more pronounced segregation in the diet when male territories are small and poor in resources at the same time. This condition would best characterise the habitat inhabited by the UAE donkey population. The data suggest that the male territories of this population are comparatively small and thus provide highly abrasive forage only.

Keywords: *Equus hemionus*, *Equus asinus*, feeding strategy, mesowear, resource partitioning

Introduction

The Asiatic wild ass *Equus hemionus* (dschiggetaj) once ranged across much of Central Asia, but is now globally threatened. The largest free-ranging populations are now restricted to an area across the Gobi desert region of Southern Mongolia. The knowledge of its distribution has been established in the last decade (WANG & SCHALLER 1996, MIX et al. 1995, 1997; READING et al. 1999, STUBBE et al. 2005). Some research was also undertaken on behavioural ecology and the systematic status of the species (BANNIKOV 1971, 1975; WOLFE 1979, MUNKHSAIKHAN et al. 1989; FEH et al. 1994). In the field of behavioural research, however, there is a gap of knowledge concerning the feeding behaviour and habitat preferences of the dschiggetaj, information that would be crucial to support conservation efforts. The mesowear method of dietary reconstruction is a fast and efficient approach to dietary reconstruction of extant and extinct ungulate populations. As a tooth-based method (KAISER et al. 2001, FORTELIUS & SOLOUNIAS 2001; KAISER 2002; FRANZ-ODENDAAL & KAISER 2003) it allows employing the extensive skeletal material collected

¹ Results of the Mongolian-German Biological Expeditions since 1962, No. 283.

in the Gobi desert area as a pathway to reveal subtle details of dietary behaviour and resource partitioning. Mesowear further has proven a suitable tool to compare dietary regimes of taxonomically closely related ungulate populations (KAISER 2003) and infer differences in food availability and habitat structure (SCHULZ et al 2007). Furthermore linking of mesowear signatures to known habitat parameters will add to our growing database of landmark populations, which are to be employed as reference for dietary reconstruction in fossil and extinct populations of ungulates including equids, but not restricted to equids. Mesowear is a measure of the attrition / abrasion equilibrium in tooth wear, and provides an average wear signal over a considerable period of the individual life span. Besides of the dietary signal the signature also encapsulates a strong environmental signal, as has been shown by KAISER (2003) and KAISER & SCHULZ (2006). FORTELIUS & SOLOUNIAS (2000) also find the mesowear signal to be not independent from the advance of overall tooth wear and thus to individual age. In general it was found, that older specimens have more blunt and round cusp apices, compared to younger individuals, where sharp cusps are more frequent. Excluding specimens in early and advanced wear may therefore calibrate for the effect of this ontogenetic sensitivity; however, the extent of variability within a population has so far never been investigated and is expected to provide demographic as well as environmental information.

Initially, the mesowear method was based on the second upper molar as a model tooth position (FORTELIUS & SOLOUNIAS 2000). KAISER & SOLOUNIAS (2003) extended the tooth model by three more maxillary tooth positions (P4, M1 and M3), which makes the method more suitable for small samples of equids, and largely enhances the resolution in large assemblages.

We apply mesowear evaluation to test the following hypotheses:

- 1: The mesowear equilibrium should reflect either differential food availability to different age classes or ontogenetic gradients in tooth wear and morphology.
- 2: Age segregation should be related to environmental conditions and dietary signals should thus reflect abiotic habitat parameters such as the local climate and geomorphology.
- 3: The mesowear equilibrium should resolve proposed sexual segregation in forage selection and availability.

Materials and Methods

We investigate cheek dentitions of *Equus hemionus* collected from 59 localities from the southern part of the Gobi desert (Bordzongijn-gobi; Mongolia) and free ranging domestic donkeys (*Equus asinus*) from 61 localities of the Musandam Peninsula (Emirate Sharjah; United Arab Emirates) (fig. 1). The material comprises 80 skulls of *E. hemionus* (41 female and 39 male) and 61 skulls of *E. asinus* (30 female and 31 males; table 1). All skulls were collected of dead animals, the carcasses of which were found in different stages of decay, most of them mummified. Collection took place in 2003 (Sharjah; United Arab Emirates) and 2001/2002 (Borzongijn-gobi; Mongolia). The Global Positioning System (GPS) was used to document geographic coordinates for each specimen. Currently the *E. hemionus* material is curated at the Museum of Domestication "Julius Kuehn" (Halle, Germany) and the material of *E. asinus* at the Zoological Museum of the University Hamburg, Germany (Appendix).

With reference to JOUBERT (1972) individuals were classified in 15 age classes based on tooth development and wear. Individuals younger than two years of age (age class 1, 2, 3, 4) were excluded from mesowear analysis because no upper permanent molars are yet in occlusion at that age. The determination of sexes was done in the field before the skulls were separated from the body. In addition, the sexual status was controlled using presence (male) and absence (female) of canines for distinction. In order to test the homogeneity and demographic structure of the sampled populations both were tested using two-sample t-test on the variable 'age class' grouped by sex. Figure 2A/B shows the demographic structure of the two populations as a box-and-whiskers plot, combined in a dual histogram with kernel density estimators. SYSTAT 11.0 software (licenced to TMK) was used to compute statistics in a MS WINDOWS XP environment.

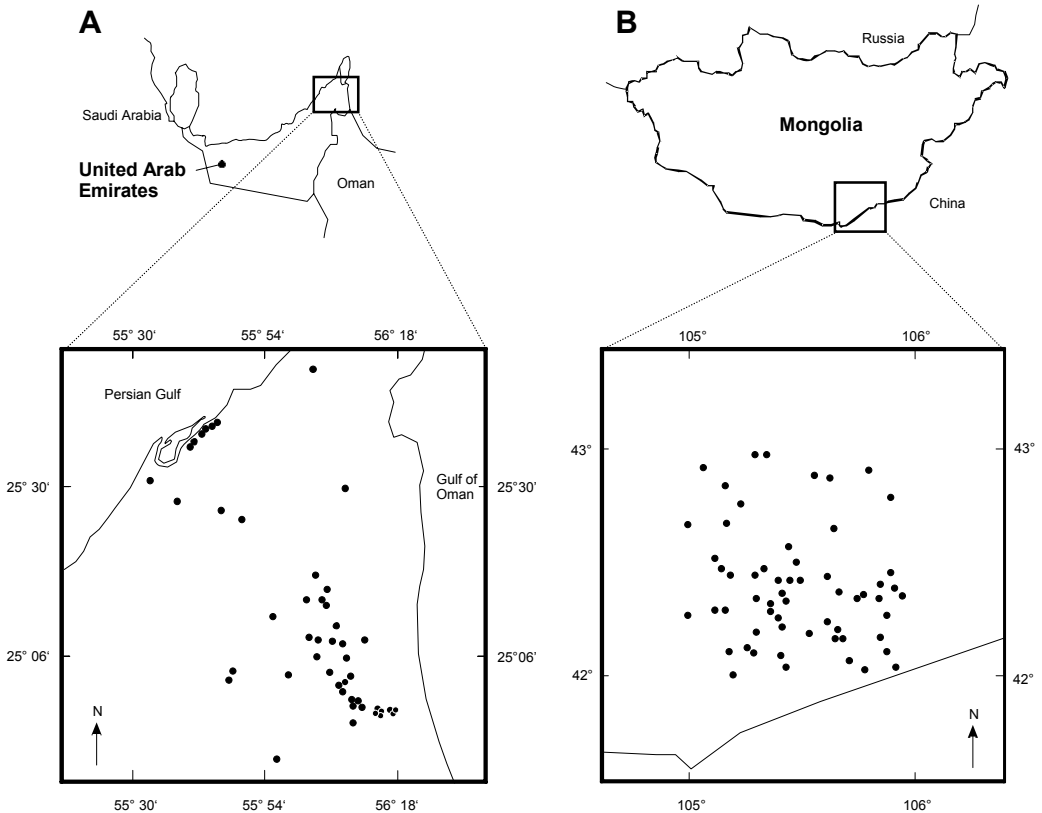


Fig. 1: Locality maps of the collecting areas. **A** = working area in the Emirate Sharjah (United Arab Emirates), **B** = working area in the Gobi Desert (Mongolia), Spots (●) indicate the collection sites of an equid individual as recorded via GPS.

Table 1: Sample structure of the two equid populations investigated (species = *E. hemionus* = dschiggetaj from the Gobi Desert (Mongolia), *E. asinus* = free ranging donkeys from the Emirate Sharjah (United Arab Emirates); SYMB = symbols used in figures to identify datasets, ea = *E. asinus*, eh = *E. hemionus*, 5-15 indicate age classes after JOUBERT (1972), n = number of specimens, age = average individual age in years, age classes determined after JOUBERT (1972), SD = standard deviation)

species	SYMB	n	age	SD
<i>E. hemionus</i>	eh ♀	41	6,89	2,961
<i>E. hemionus</i>	eh ♂	39	6,00	2,936
<i>E. asinus</i>	ea ♀	30	4,68	3,514
<i>E. asinus</i>	ea ♂	31	7,07	3,404

Mesowear technique

We employed the replica technique to mould tooth apices of upper post canine cheek tooth rows. After cleaning specimens with acetone and vanish remover (HAYEK et al. 1992), a contact layer was made using Provil novo Light C.D. (Heraeus Kulzer) polysiloxane dental moulding compound. A support layer was added (Provil novo Putty, Heraeus Kulzer). Replicas were reversed using

epoxy resin Injektionsharz EP (Reckli-Chemiewerkstoff Co., Herne). The mesowear method was employed following FORTÉLIUS & SOLOUNIAS (2000). This methodology treats ungulate tooth mesowear as two variables: 1. occlusal relief and 2. cusp shape. Occlusal relief (OR) is classified as high (h) or low (l), depending on how high the cusps rise above the valley between them. Occlusal relief is referred to as percentages; %high and %low result in 100%, therefore only %high is given (Tab. 2). The second mesowear variable, cusp shape, includes 3 scored attributes: sharp (s), round (r) and blunt (b) according to the degree of facet development. Cusp shape is also referred to as percentage (Tab. 2). FORTÉLIUS & SOLOUNIAS (2000) restricted their study of ungulate mesowear to the upper M2. Here we include upper M3 and M2 as suggested by KAISER (2003). Eighty eight teeth (50 M2 and 38 M3) of *E. hemionus* and 164 teeth (84 M2 and 80 M3) of *E. asinus* were available for this investigation (see Appendix).

Table 2: Mesowear datasets of *Equus hemionus* (eh) from Mongolia and of *Equus asinus* (ea) from the Emirate Sharjah (UAE)

(SYMB = symbols used in figures to identify datasets, printed in bold indicate significance ($p \leq 0.06$). %h = percent high occlusal relief, %r = percent round cusps, %b = percent blunt cusps (after FORTÉLIUS & SOLOUNIAS 2000), n = number of observations, p = significance of Pearson Chi-Square of %h, %s, %b, n. a. = not available. Ea = *E. asinus*, eh = *E. hemionus*, 5-15 indicate age classes after JOUBERT (1972), (mean) = species average)

Dataset	SYMB	%h	%s	%r	%b	n	p
1	eh (mean)	47,4	4	85,7	10,3	175	< 0,001
2	ea (mean)	55,4	43,5	39,1	17,4	184	< 0,001
3	eh ♀	47,8	3,3	81,5	15,2	92	< 0,001
4	eh ♂	57,8	4,8	90,4	4,8	83	< 0,001
5	ea ♀	57,5	47,9	45,2	6,8	73	< 0,001
6	ea ♂	52,9	41,2	32,4	26,5	102	0,187
7	eh5	16,7	16,7	83,3	0	6	0,102
8	eh6	100	0	100	0	2	n. a.
9	eh7	60	0	80	20	5	0,180
10	eh8	66,7	0	100	0	9	0,317
11	eh9	85,7	0	100	0	28	< 0,001
12	eh10	62,5	8,3	91,7	0	24	< 0,001
13	eh11	55,3	4,3	89,4	6,4	47	< 0,001
14	eh12	33,3	4,8	83,3	11,9	42	< 0,001
15	eh13	0	0	0	100	6	n. a.
16	eh15	0	0	0	100	3	n. a.
17	ea5	100	16,7	83,3	0	6	0,102
18	ea6	100	71,4	28,6	0	7	0,257
19	ea7	83,3	50	50	0	6	0,102
20	ea8	80	40	40	20	10	0,058
21	ea9	74,2	61,3	32,3	6,5	31	< 0,001
22	ea10	52,9	41,2	47,1	11,8	17	0,161
23	ea11	37,8	43,2	43,3	13,5	37	0,038
24	ea12	40	32,5	35	32,5	40	0,206
25	ea13	50	50	50	0	4	1,000
26	ea14	37,5	37,5	12,5	50	8	0,417
27	ea15	50	0	25	75	4	0,317

We computed hierarchical cluster trees with complete linkage (furthest neighbours) based on Euclidean Distance, and principle components analysis of the factors %h, %s, and %b. As a clustering algorithm the standard hierarchical amalgamation method by HARTIGAN (1975) was applied. The algorithm of GRUVAEUS & WEINER (1972) was used to order the cluster tree. As a comparative dataset for dietary classification, a set of 27 extant ungulate species was used following FORTELIUS & SOLOUNIAS (2000). We also follow FORTELIUS & SOLOUNIAS's classification of extant species into three broad dietary classes: browser, mixed feeder and grazer.

Results

Demographic structure

In the age class distribution, we observe a high degree of similarity between the two equid populations. We find the majority of individuals to represent the two major age classes 11 (7-9 years) and 12 (9-11 years) after JOUBERT (1972) (fig. 2A/B). The average individual age in the *E. asinus*-population is 5.9 and 8 years in the *E. hemionus*-population (table 1). It is thus evident that members of the *E. hemionus*-population were 2 years older at death. Two-sample t-test (Bonferroni adjusted) statistic is applied. Female members of the *E. asinus*-population are significantly ($p = 0.009$) older (4.7 years) than males (7.1 years). In the *E. hemionus*-population the females' (6.9 years) and males' age averages (6 years) are close ($p = 0.181$).

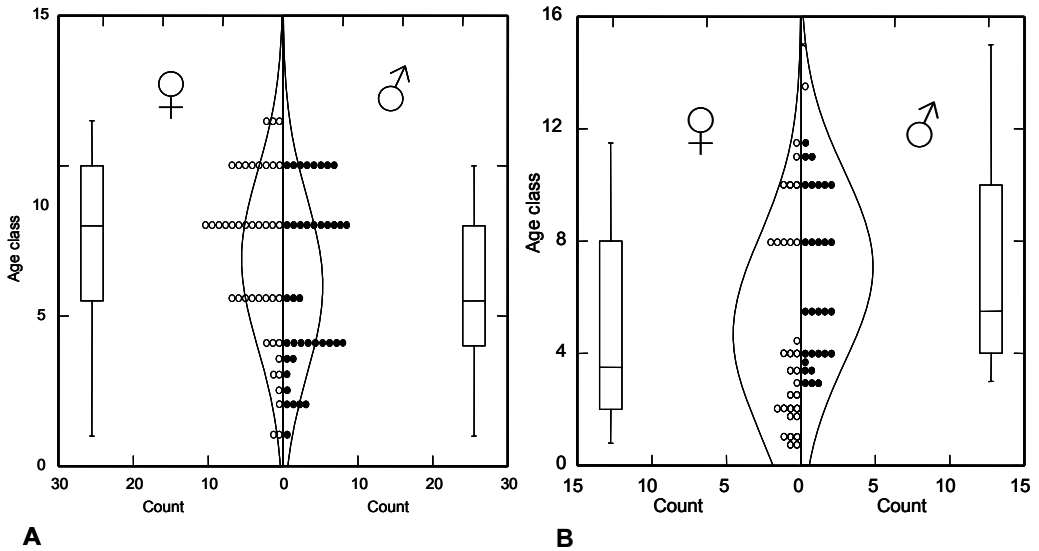


Fig. 2: Combined plot showing age classes statistics. Dual histogram plots (\circ = female, \bullet = male) and kernel density estimators indicate frequencies of male and female individuals representing a specific age class after (JOUBERT, 1972). Box and whisker plots give the sample median, and quartiles for each group (*E. hemionus* [2A] and *E. asinus* [2B]).

Dietary evaluation

The combination of principal components analysis (PCA) and cluster analysis allows highly resolving discrimination of dietary traits (fig. 3A, B). In each PCA the two principal components represent minimum 90% of the total variance. The pattern of the cluster tree (fig. 3B) is represented by circumscribing lines in the PCA factor plot (fig. 3A). Within the dietary spectrum represented by the comparative species, the dschiggetajs from the Gobi (*E. hemionus*-population) classify as grazers in close proximity to *Alcelaphus buselaphus* (ab) and *Hippotragus niger* (hn) (fig. 3A). The feral donkeys from the UAE (*E. asinus*-population) show a grazing signature as indicated by their close linkage to the wildebeest (*Connochaetes taurinus*; ct) and the hartebeest (*Alcelaphus buselaphus*; ab), two grazing African alcelaphines (fig. 3A).

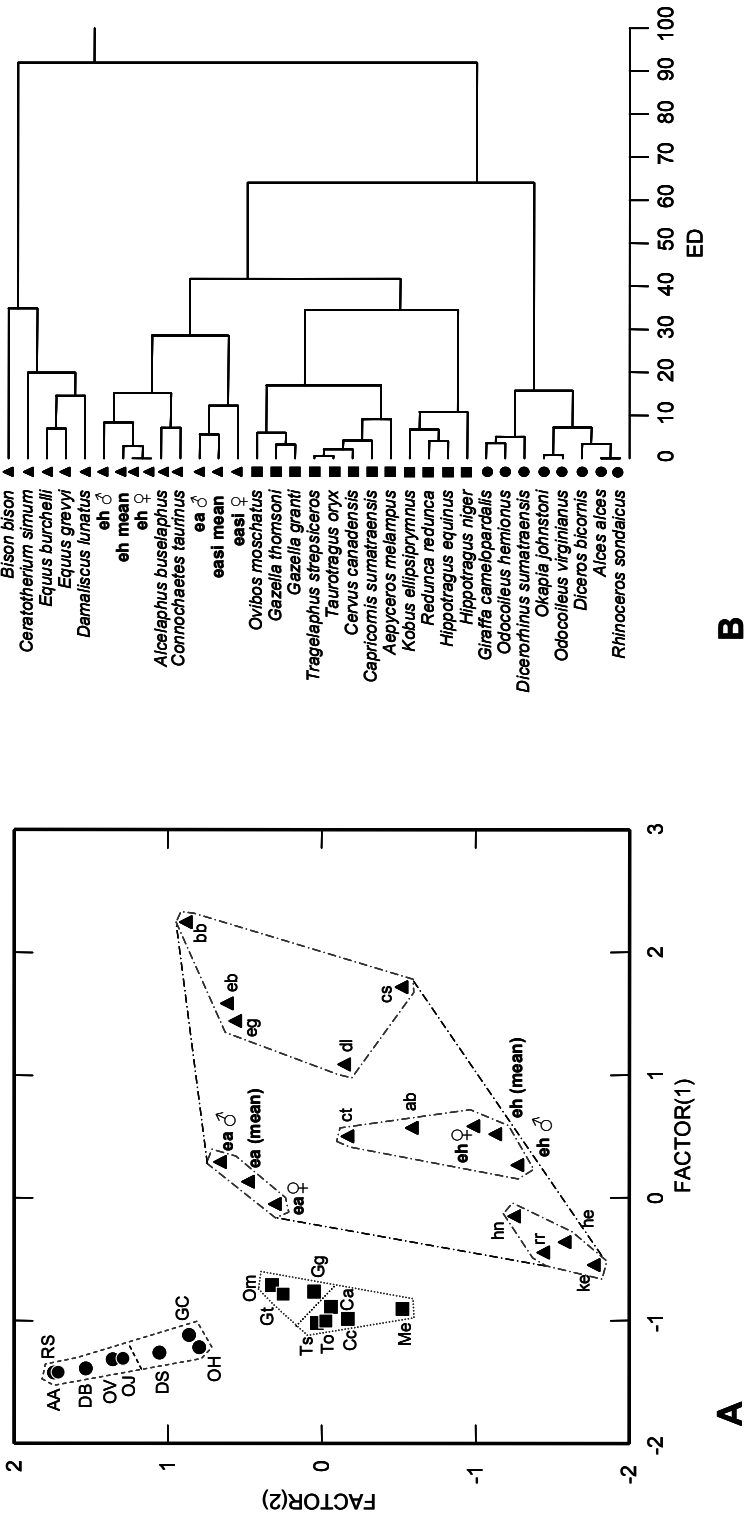


Fig. 3: Principal components analysis (PCA) (A) and cluster tree (B) based on mesowear parameters %h, %s and %b depending on sexual segregation. Factor (1) represents 75.86% and factor (2) 18.38 % of the total variance. Dashed line indicates factor space occupied by browsers (circle), dotted line = mixed feeders (rectangles), dot-dashed line = grazers (triangles); identification tags of *Equus hemionus*, mean = average dataset representing both sexes.

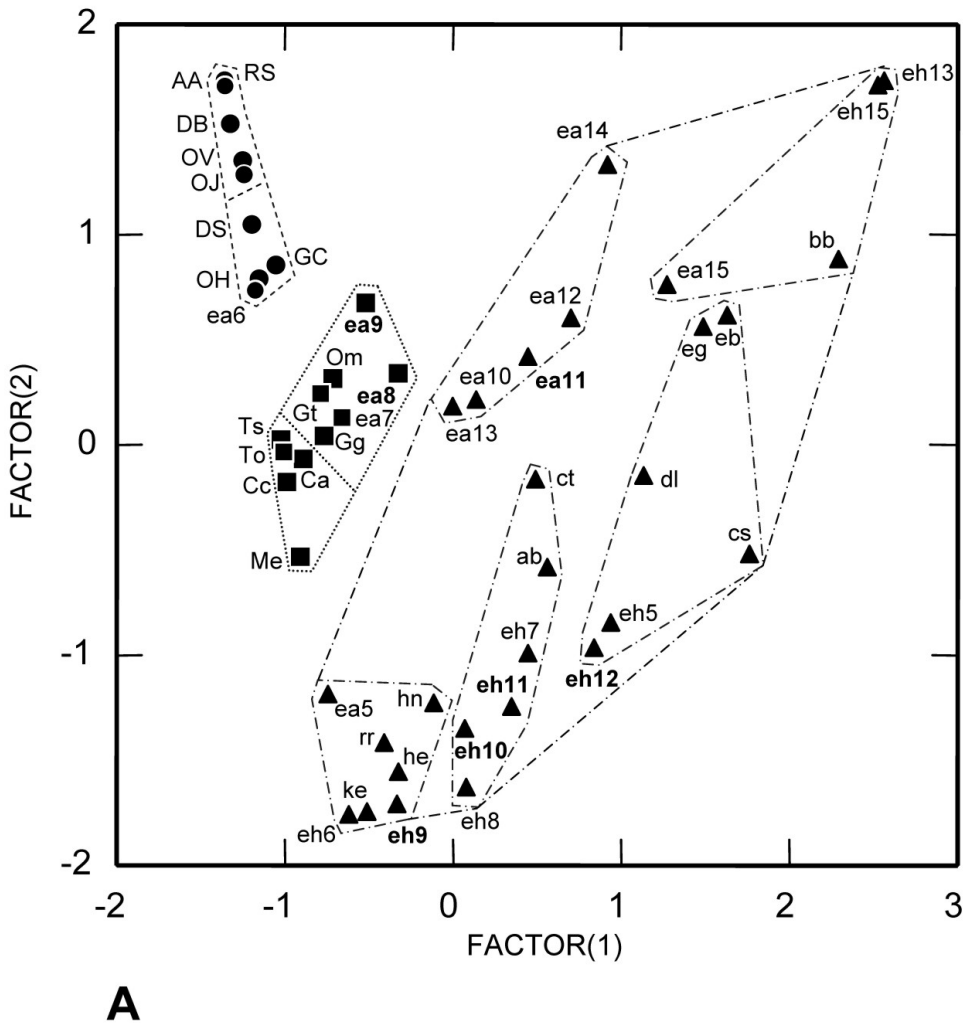


Fig. 4A: Principal components analysis (PCA) and cluster tree based on mesowear parameters %h, %s and %b depending on individual age. Factor (1) represents 70.51 % and factor (2) 20.17 % of the total variance. Dashed line indicates factor space occupied by browsers (circle), dotted line = mixed feeders (rectangles), dot-dashed line = grazers (triangles); identification tags of *Equus* populations investigated set in bold (table 2); ea = *E. asinus*, eh = *Equus hemionus*, 5-15 indicate age classes after JOUBERT (1972), (for figs. 4b & c see next page).

The average mesowear signal of both *Equus* populations (eh mean and ea mean) is further found to be less abrasion-dominated compared to the two African zebra species, the plains zebra (*Equus burchellii*; eb) and the Grevy's Zebra (*Equus grevy*; eb). Bar charts (fig. 5A-F) show frequencies of cusp shape and occlusal relief parameters (%l, %h, %s, %r and %b). In comparing the two population's means (fig. 5A, D) it becomes obvious that the dschiggetaj has a more abrasive diet than the donkeys. This is indicated by more round cusps (eh mean %r = 85.7/ea mean %r = 39.1) at the expense of sharp cusps (eh mean %s = 4/ea mean %s = 44.5) (fig. 5A, D). Also it is observed that the dschiggetaj has a lower relief than the donkeys.

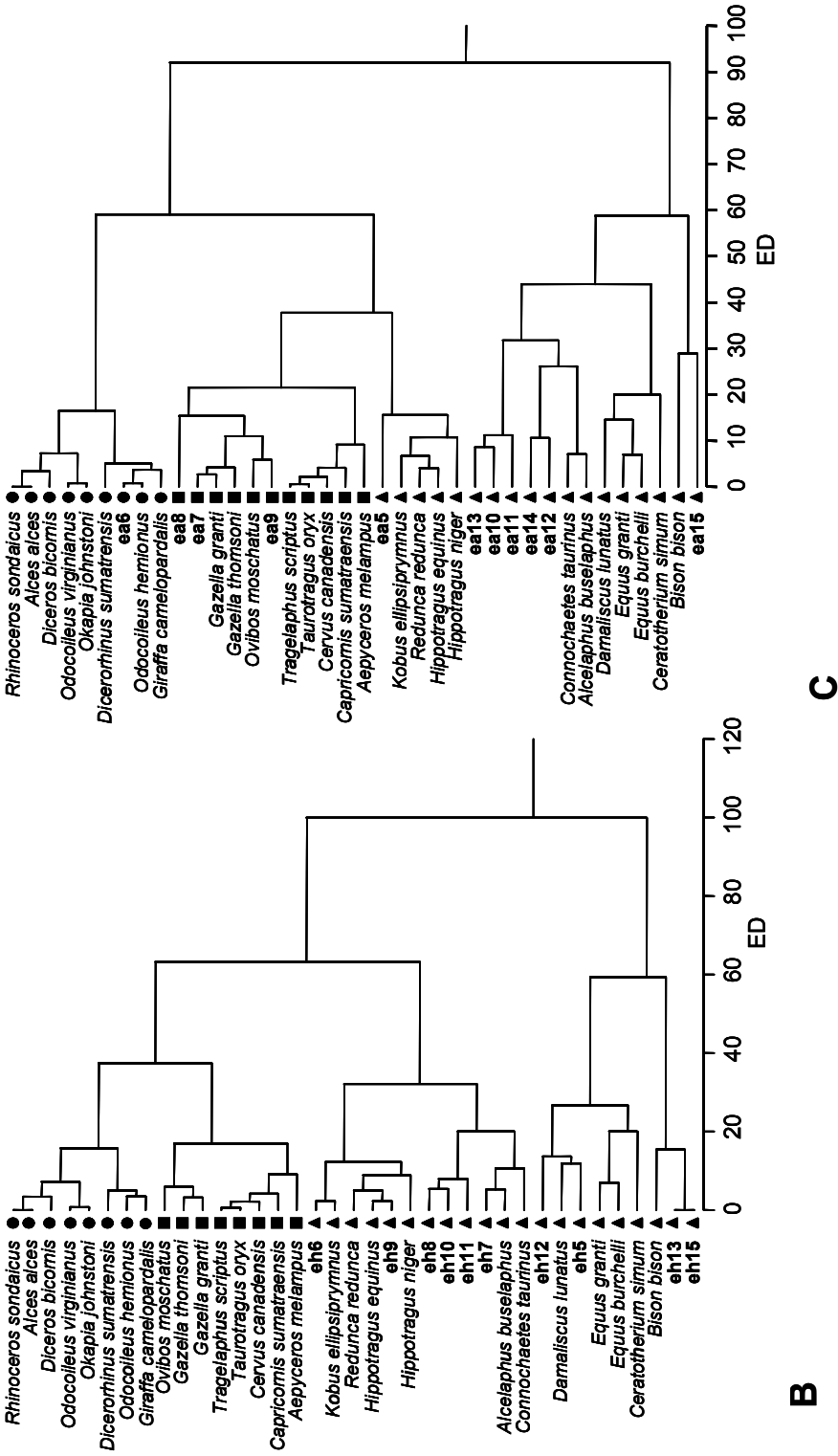


Fig. 4B, C: Hierarchical cluster tree based on mesowear parameters %h, %s and %b classifying *Equus asinus* (ea) age classes 5 to 15 after JOUBERT (1972) (datasets 7 to 16 - **B** and datasets 18 to 27 - **C** as given in table 2) and a set of 27 comparison species classified as “typical” according the dietary categories by FORTÉLIUS & SOLOUNIAS (2000); browsers = circles, mixed feeder = rectangles, grazer = triangles; ED = Euclidean distance (root-mean-squared difference).

Sexual segregation in the two equids is found to be rather small as both sexes plot close to the population means (fig. 3A). In the dschiggetaj sample males differ more from the population mean (eh mean) than females (fig. 3B). In *E. hemionus* females less round cusps are observed than in males, while females have more blunt cusps and males' teeth are less blunt (eh ♀ %b = 15.2, %r = 81.5, eh ♂ %b = 4.8 and %r = 90.4). The same trend is evident in the occlusal relief parameters. Females have lower reliefs than males (eh ♀ %h = 47.8, eh ♂ %h = 57.8). This indicates that *E. hemionus* males (fig. 5B) have a more attrition-dominated dietary signal than the females (fig. 5C). In *E. asinus* females have more sharp and less blunt cusps than males (ea ♀ %s = 47.9, %b = 6.8 and ea ♂ %s = 41.2, %b = 26.5), which indicates a less abrasion-dominated mesowear signature in female feral donkeys compared to males.

E. hemionus has a grazing signal in all age classes (fig. 4A, C). It is obvious that with increasing age the mesowear signature shifts to the abrasion dominated end of the spectrum. In the dschiggetaj, age classes 9-12 (table 2) are closely linked ($p < 0.001$) to the grazing *Alcelaphus buselaphus* (ab). The oldest *E. hemionus* individuals (age class 15) cluster close to the American Plains bison (*Bison bison*, bb) at the abrasion dominated end of the mesowear continuum (fig. 4C). In general there is more abrasion control in old than in young individuals. The same general observation applies for *E. asinus* (fig. 4A, B). In contrast to *E. hemionus*, it is observed that young individuals of *E. asinus* (age classes ea 8 to 9) are classified together with mixed feeding ruminant species such as the Grant's gazelle (*Gazella granti*; Gg), the Thomson gazelle (*Gazella thomsoni*; Gt) and the musk ox (*Ovibos moschatus*; Om).

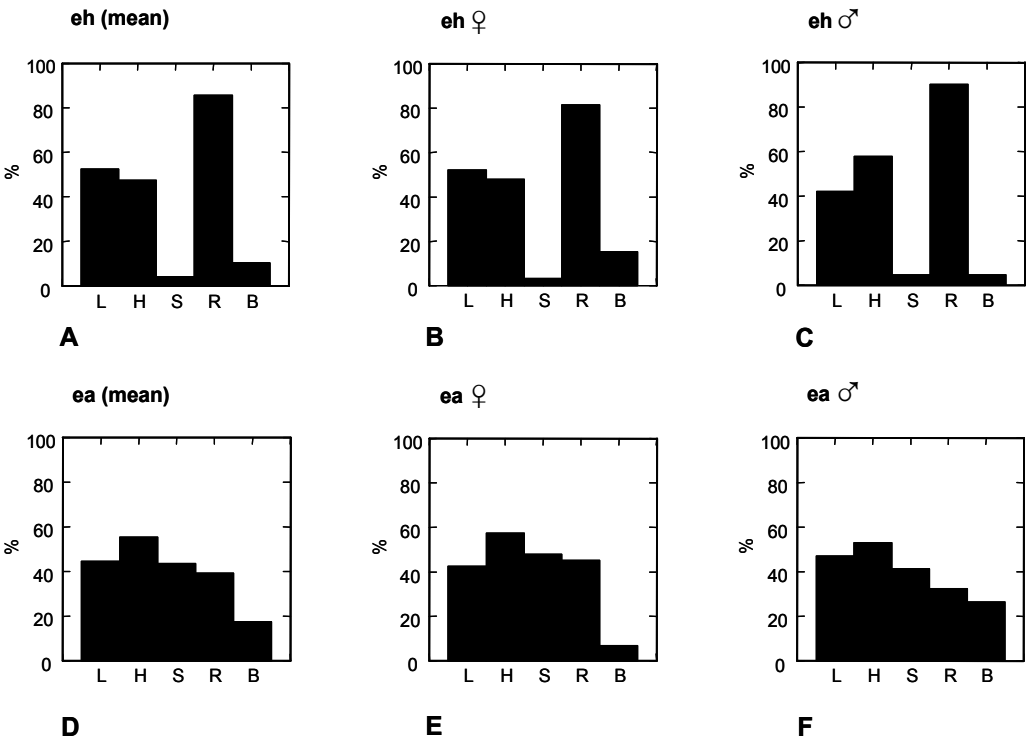


Fig. 5A-F: Bar charts of mesowear parameters; L = % low, H = % high, S = % sharp, R = % round and B = % blunt; symbols refer to dataset as given in table 2, ea = *E. asinus*, eh = *Equus hemionus*, mean = average dataset representing both sexes.

Discussion

Compared to the two African Zebra species employed for comparison (*E. burchellii* and *E. grevyi*), the average signatures of *E. hemionus* from the Gobi desert and *E. asinus* from the UAE suggest a less abrasion-dominated diet. In accordance with our hypothesis # 1, we observe a shift towards more abrasion control in the mesowear equilibrium with increasing individual age. This signal is consistent with observations that lead FORTELIUS & SOLOUNIAS (2000) to suggest mesowear to be an ontogenetically sensitive approach. Our results confirm this sensitivity. However, differences between populations in a single age class can not be explained by this effect. Especially in younger individuals of *E. asinus* a mesowear signature is realized, that equals that of a mixed feeder, while the average mesowear signature of both populations is that of a grazer. While the widely scattered mesowear signature in the age classes of both species support our hypothesis # 2. This indicates that in the UAE habitat equids had access to less abrasive forage than *E. hemionus* had in the Gobi habitat in all age classes.

Additionally we thus hypothesise that the diet available to the *E. asinus*-population is more heterogeneous and less abrasive than that available to the *E. hemionus*-population and should reflect the differences in vegetation structure between the Arabian and the Mongolian habitat. The habitat of the *E. asinus* population investigated is an enclosed area that is bordered by the Omani mountains in the east, by the Persian Gulf in the West and by the Arabian Desert in the south. It has a mosaic structure, as it includes the western slopes of the mountains, the Al-Madam plain and the coastal area of the Emirate Sharjah (TURNBULL et al., 2002). The Al-Madam plain receives the same annual precipitation (100 mm) as the Gobi desert habitat of the dschiggetaj. The habitat however has more anthropogenous resources available to the donkeys than the Gobi habitat has to the dschiggetaj population. These are frequent palm gardens supplied with wells and open water basins, which are surrounded by a permanent vegetation cover. This makes the habitat in the UAE a more diverse mosaic of feeding resources compared to the Mongolian habitat of *E. hemionus*. The Mongolian habitat is an open steppe environment the vegetation of which is dominated by a fine-leaved grass (*Stipa gobica*), shrubs (*Amygdalus mongolica* and *Zygophyllum xanthoxylon*) and onions (*Allium mongolicum*) (ZHIRNOV & ILYIN-SKY 1986, READING et al. 2001, STUBBE et al. 2005).

Silica phytoliths and grit particle make the available forage comparatively abrasive. Owing to these habitat characteristics, we interpret the more abrasion-dominated signature of the *E. hemionus* mean dataset as to reflect the differential food availability in the two habitats and thus to support our hypothesis # 1.

It is realized, that in both populations sexes show more intraspecific differences in mesowear than there is interspecific difference between the two African zebra species *E. burchellii* and *E. grevyi*. Studies by MOEHLMANN (1974, 1979, 1998) indicate that resource quality and feeding ecology of feral donkey is reflected by the social structure. According to studies by RUBEN-STEIN on feral horses from the Shackleford Banks (1981, 1986, 1994) the social systems in equids are more complex and not species-specific as KLINGEL (1975) suggests. MOEHLMANN (1998) suggests that in arid habitats males tend to be more territorial than in mesic habitats. Females would then compete for the males with the best territory. If our hypothesis # 3 were correct, one would expect territorial males to have less variety in food resources due to the more restricted feeding area. Food resources in a restricted area under dry habitat conditions, however would be more intensively exploited and thus result in foraging closer to the ground where forage is more grit contaminated. This would result in increased abrasive tooth wear. Given the case that the territory is small, this effect should be even more pronounced. One would then expect a more pronounced sexual segregation in dietary resource partitioning if male territories are small and poor in resources at the same time. This condition would best characterise the territory inhabited by the *E. asinus* population in the UAE (7000 individuals according to TURNBULL et al., 2002), which inhabit the highly restricted area of 5424 km². This should result in small male territories and thus we find our hypothesis # 3 supported by the

mesowear data which suggest highly abrasive forage for the male donkeys from the UAE. We therefore realize that the two populations inhabiting semi-desert environments at similar precipitation rates show behavioural patterns that cause a characteristic signature in sexual dietary segregation, which is related to the specific geo-demographic situation as the most crucial parameters to resource availability. It is also realized that mesowear may resolve subtle patterns in dietary resource partitioning as an inexpensive and fast pathway to a better understanding of habitat interactions of wild ranging ungulates. The use of extensive museum material in combination with field collections of skeletal remains may thus open up a new source of conservation-relevant information that may be crucial for a better understanding of population dynamics, such as home range and territory size, in particular in those species, which are difficult to observe in the wild. Further studies could ponder on the flexibility and variability of:

1. dietary habits,
2. social structure in relation to habitat structure,
3. resource partitioning in age classes and sexes.

Comparison of populations bound to different habitat settings will then allow us to better estimate the stability of a threatened population.

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Appendix

Dental specimens of *Equus asinus*

Second upper molars

UAE-S55, UAE-S68, UAE-S8, UAE-S24, UAE-S46, UAE-S64, UAE-S10, UAE-S17, UAE-S19, UAE-S58, UAE-S74, UAE-S11, UAE-S13, UAE-S15, UAE-S22, UAE-S50, UAE-S60, UAE-S63, UAE-S73, UAE-S16, UAE-S33, UAE-S41, UAE-S61, UAE-S70, UAE-S18, UAE-S44, UAE-S49, UAE-S5, UAE-S53, UAE-S56, UAE-S6, UAE-S65, UAE-S69, UAE-S72, UAE-S20, UAE-S21, UAE-S29, UAE-S31, UAE-S35, UAE-S39, UAE-S45, UAE-S47c, UAE-S54, UAE-S59, UAE-S71, UAE-S40, UAE-S52, UAE-S57, UAE-S51

Third upper molars

UAE-S8, UAE-S17, UAE-S58, UAE-S74, UAE-S11, UAE-S12, UAE-S13, UAE-S15, UAE-S50, UAE-S60, UAE-S63, UAE-S73, UAE-S16, UAE-S33, UAE-S41, UAE-S61, UAE-S70, UAE-S18, UAE-S26, UAE-S44, UAE-S49, UAE-S5, UAE-S56, UAE-S69, UAE-S72, UAE-S20, UAE-S21, UAE-S29, UAE-S31, UAE-S39, UAE-S45, UAE-S47c, UAE-S54, UAE-S59, UAE-S71, UAE-S40, UAE-S52, UAE-S57, UAE-S51

Dental specimens of *Equus hemionus*

Second upper molars

JKMH-39, JKMH-46, JKMH-115, JKMH-25, JKMH-26, JKMH-63, JKMH-107, JKMH-23, JKMH-28, JKMH-33, JKMH-105, JKMH-100, JKMH-98, JKMH-95, JKMH-91, JKMH-66, JKMH-64, JKMH-4, JKMH-3, JKMH-11, JKMH-15, JKMH-17, JKMH-41, JKMH-43, JKMH-112, JKMH-117, JKMH-8, JKMH-14, JKMH-29, JKMH-34, JKMH-38, JKMH-40, JKMH-42, JKMH-50, JKMH-58, JKMH-59, JKMH-109, JKMH-110, JKMH-99, JKMH-114, JKMH-97, JKMH-119, JKMH-72, JKMH-70, JKMH-69, JKMH-62, JKMH-61, JKMH-7, JKMH-13, JKMH-19, JKMH-20, JKMH-24, JKMH-27, JKMH-35, JKMH-37, JKMH-47, JKMH-48, JKMH-49, JKMH-51, JKMH-108, JKMH-111, JKMH-104, JKMH-101, JKMH-103, JKMH-102, JKMH-118, JKMH-68, JKMH-71, JKMH-5, JKMH-9, JKMH-10, JKMH-12, JKMH-16, JKMH-18, JKMH-32, JKMH-36, JKMH-44, JKMH-45, JKMH-52, JKMH-56, JKMH-65, JKMH-22, JKMH-30, JKMH-31, JKMH-54

Third upper molars

JKMH-25, JKMH-26, JKMH-63, JKMH-23, JKMH-28, JKMH-33, JKMH-105, JKMH-100, JKMH-98, JKMH-95, JKMH-91, JKMH-66, JKMH-64, JKMH-4, JKMH-3, JKMH-11, JKMH-15, JKMH-17, JKMH-41, JKMH-43, JKMH-112, JKMH-117, JKMH-8, JKMH-14, JKMH-29, JKMH-34, JKMH-38, JKMH-40, JKMH-42, JKMH-50, JKMH-58, JKMH-59, JKMH-109, JKMH-110, JKMH-99, JKMH-114, JKMH-97, JKMH-96, JKMH-119, JKMH-72, JKMH-70, JKMH-69, JKMH-62, JKMH-61, JKMH-7, JKMH-13, JKMH-19, JKMH-20, JKMH-24, JKMH-27, JKMH-35, JKMH-37, JKMH-47, JKMH-48, JKMH-49, JKMH-51, JKMH-108, JKMH-111, JKMH-104, JKMH-101, JKMH-103, JKMH-102, JKMH-118, JKMH-68, JKMH-71, JKMH-5, JKMH-9, JKMH-10, JKMH-12, JKMH-16, JKMH-18, JKMH-32, JKMH-36, JKMH-44, JKMH-45, JKMH-52, JKMH-56, JKMH-65, JKMH-22, JKMH-30, JKMH-31