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Feeding selectivity for diet abrasiveness in sheep and goats

Nicole L. Ackermans[a,*], Louise F. Martin[a], Jürgen Hummel[b], Dennis W.H. Müller[c], Marcus Clauss[a], Jean-Michel Hatt[a]

[a] Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, CH-8057, Zurich, Switzerland
[b] Department of Animal Sciences, Ruminant Nutrition, Georg-August-University, Göttingen, D-37075, Germany
[c] Zoologischer Garten Halle GmbH, D-06114, Halle (Saale), Germany

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ABSTRACT

Tooth wear can be a considerable factor in shortening the lifespan of herbivores. It is mainly caused by the ingestion of silica particles, either phytoliths - internal to the ingested plants - or external abrasives, such as dust or grit. The avoidance of these abrasives can therefore be favourable to maintain healthy teeth, though it is not known to what extent herbivores are able to select diets based on the level of abrasive contamination. In order to better understand herbivores' selective capabilities, controlled feeding trials were performed on goats and sheep, offered a choice between high- and low-abrasive pelleted diets. Adding coarse grit resulted in the goats avoiding the diet, whereas the addition of finer dust, yet in high proportion, did not elicit any diet preference response in the sheep. Though preliminary, the experimental results provide an insight into the possible reactions of goats and sheep in response to dietary contamination by external abrasives and suggest that below a certain grain size, abrasives may no longer be detectable by these animals.

1. Introduction

One of the main factors capable of shortening herbivore's natural lifespan is excessive tooth wear (Janis and Fortelius, 1988). The principal culprits contributing to dental wear are silica particles from the herbivore's natural diet that can either be encapsulated in plant matter in the form of opaline silicates called phytoliths, or that can be ingested as external abrasives in the form of dust and grit. Grasses high in phytolith content are the principal component of grazer diets, subjecting these animals to especially high amounts of wear (reviewed by Damuth and Janis, 2014; Healy, 1967; Hummel et al., 2011). Evolutionary adaptations such as hypsodonty suggest a high value in avoiding large amounts of abrasives and therefore point out that the ability to detect abrasiveness may influence ruminant feeding behaviours (Massey et al., 2009) and serve as an intentional control for the reduction of dental wear.

Food choice experiments in voles (*Microtus orchogaster)* demonstrated an avoidance of high silica content grasses (Gali-Muhtasib et al., 1992; Massey and Hartley, 2006). The presence of abrasives was found to be tolerated in guinea pigs (*Cavia porcellus*) (Müller et al., 2015) and rabbits (*Oryctolagus cuniculus*) fed diets of varying abrasiveness (Müller et al., 2014), although other studies on rabbits (Cotterill et al., 2007) show a reduction of preference for plants with above-average silica rates.

It has also been suggested that ruminants should avoid the ingestion of abrasive feeds (Hindelang and Peterson, 1993), though studies testing this assumption are rare. Shewemaker et al. (1989) determined dietary preference of ewes and lambs for different forage species during different seasons. Grass species preference varied depending on phenological stages, though when silicon was measured no preference was found. In a later study, Massey et al. (2009) assessed the preference of sheep by manipulating silica levels of five grass species. Again, preference was driven by grass species rather than silica levels within species.

In other demonstrations of silicate avoidance, animals have been observed to prefer removing grit by washing their food before eating it. This has been the case with primates (Allritz et al., 2013; Visalberghi and Fragaszy, 1990), suids (Ito et al., 2017; Sommer et al., 2016) and otters (Neunteufel, 2007). Even in humans, chewing intensity was reduced in the presence of external abrasives added to chewing gum (Prinz, 2004), an observation also seen in chimpanzees (*Pan troglodytes verus*) (Schulz-Kornas et al., 2019). A current representation of the detrimental effects of tooth wear is clearly visible in the livestock industry, where excessive tooth wear is at the root of considerable

* Corresponding author at: Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstrasse 260, 8057, Zurich, Switzerland.

E-mail address: nicole.ackermans@uzh.ch (N.L. Ackermans).

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economic loss for sheep and goat farmers. In sandy feeding pastures considered areas of high wear, ewes are often culled from flocks at an early age, being no longer able to graze efficiently due to excessively worn down teeth (Erjavec and Crossley, 2010). This occurrence was first studied by Healy and Ludwig (1965), when New Zealand sheep feeding on highly eroded pastures consumed above-average amounts of soil (up to 400 g/day), which was linked to high amounts of wear (recorded by incisor length). Extreme tooth wear can result in numerous pathologies, such as loss of teeth or premature mortality, reducing the ewes' reproductive lifespan and impacting production in sheep (McGregor, 2011) as well as in goats (McGregor and Butler, 2011). While soil erosion may be caused by high stocking rates, it can also be impacted by climate and vary with the seasons (Madden, 2014). To what extent sheep and goats actively avoid external abrasives, when given a choice, is still unknown.

We conducted a controlled feeding experiment on goats and sheep, by providing a choice of more or less abrasive feeds to observe preference selection. We predicted the animals to avoid the added-abrasives diet, implying that small ruminants are able to influence their own diet when it comes to abrasiveness selection, and thus reduce tooth wear.

2. Material and methods

2.1. Animals and husbandry conditions

The goats partaking in this dietary preference trial were part of a long-term tooth wear experiment (Ackermans et al., 2018) during which a short preference trial was performed. With approval by the Swiss Cantonal Animal Care and Use Committee Zurich (animal experiment license N°115/2009), five female goats (*Capra aegagrus hircus*) of mixed age, weight and breed (four Saanen goats and a Chamois Coloured goat; average body mass: 60 ± 8 kg, estimated age: 3–10 years, exact ages unknown) were subjected to a choice trial during which they were provided with two different pelleted feeds. Prior to the experiment, these animals had been fed a pelleted diet consisting of grass hay, rice hulls and sand (GRS), and a minimum allotment of grass hay for five months. At the time of the food preference trial, each animal was isolated in a concrete-floored pen and provided with access to two feeding boxes, one containing 500 g of the GRS diet, and one containing the same pelleted diet but without added sand, for two minutes. The amount of feed consumed was determined by weighing the boxes before and after the experiment. The experiment was repeated four times over one day for each individual.

A second experiment was performed on sheep (*Ovis aries*); also as part of a long-term tooth wear experiment during which a period was dedicated to preference trials. The animal experiments were performed with approval of the Swiss Cantonal Animal Care and Use Committee Zurich (animal experiment license N° 10/2016). Thirteen ewes of mixed age, weight and breed (average body mass: 75 ± 16 kg, estimated age: 4–10 years; exact ages unknown) were subjected to a feeding trial during which they were provided with a choice of eight different pelleted feeds (Table 1). At the time of the food preference trial, each animal was isolated in a concrete-floored feeding pen (10 m^2) allowing nose-to-nose contact with the other sheep through the barrier to reduce stress. Each individual had equal access to seven buckets, containing 500 g of each diet. A timer was set off once the animal started eating and observation ensued for 10 min. The amount of feed consumed was determined by weighing the buckets before and after the experiment. The order of the food was changed between repetitions to avoid any positional preference. The experiment was repeated seven times across four months for each individual.

2.2. Experimental diets

The pellet base of the experimental diet used in the experiment on goats was composed of grass hay and rice hulls, with or without the addition of "playground sand" (REDSUN garden products B.V., Heijen, Denmark; grain size 0–1 mm, mean particle size of 233 μm measured by sieve analysis). During diet production, the proportion of indigestible abrasives in the GRS diet was designed to be mimicked in the other diet by a similar proportion of indigestible, non-abrasive filler, in order to provide comparable levels of energy per amount of pellets (see nutritional analysis in Müller et al. (2014)). The animals had previously been maintained on the GRS diet for five months.

In the experiment performed with sheep, seven experimental pelleted diets of increasing abrasiveness levels were formulated to be isocaloric and isonitrogenic. The pellets had a base of lucerne meal, which contains no phytoliths. Diets were designed to represent a spectrum of abrasive sizes and concentrations. External abrasives were added in the form of silica dust in three different sizes: small, medium and large abrasives (SCR-Sibelco N.V., Antwerp, Belgium. Small abrasives: SIRCON® M500, mean particle size of 4 μm; medium abrasives: MICROSIL® M4, mean particle size of 50 μm; large abrasives: METTET AF100, mean particle size of 130 μm). For each diet of a different abrasive size, abrasives were added in two concentrations [4%] and [8%], resulting in seven different diets: small abrasives [4%], small abrasives [8%], medium abrasives [4%], medium abrasives [8%], large abrasives [4%], large abrasives [8%] and a control diet with no abrasives (Table 1). The two groups of sheep used in this experiment had been kept for seven months on the "control diet" and the "large abrasives [8%] diet", respectively.

2.3. Statistical analysis

All analyses were performed in SPSS 22.0 (IBM, Armonk, NY, USA) with the significance level set to $P < 0.05$. For the goats, comparisons between individuals were performed using a paired *t*-test. For the sheep, data were expressed as proportion of the total intake per session for each diet, so as to avoid spurious effects due to differences in the total amount eaten per session, and either used with the data of all repetitions (13 animals from two groups, 7 diets, 4 repetitions = 364 data points) or with an average value per individual per diet (13 animals from two groups, 7 diets = 91 data points). As data were not normally distributed, General Linear Models (GLMs) with ranked data were performed. GLMs included the proportion of intake as the dependent variable, and either group and diet, or group, abrasive size and abrasive concentration as independent factors.

3. Results

For the goats, the paired *t*-test showed a significant difference between diets ($P = 0.017$, $t = 3.955$; df = 4), showing a higher consumption for the diet without added abrasives (Fig. 1).

For the sheep experiment, using data for all individual repetition experiments and diets, there was no significant difference between diets ($F = 1.571$, $P = 0.155$) or groups ($F = 0.378$, $P = 0.539$), with no significant diet * group interaction ($F = 1.738$, $P = 0.111$); similarly, there was no significant effect of abrasive size ($F = 1.086$, $P = 0.339$), abrasive concentration ($F = 0.027$, $P = 0.869$), or groups ($F = 0.056$, $P = 0.814$), but the abrasive size * abrasive concentration interaction was significant ($F = 3.931$, $P = 0.020$), indicating that differences between abrasive concentration were not the same for all abrasive sizes. Whereas intake was lower for the "small abrasives [8%]" diet, intake was higher for the "medium abrasives [8%]" and "large abrasives [8%]" diets compared to the respective [4%] diets (Fig. 2).

Using average data from the four repetition experiments for each diet, there was no significant difference between diets ($F = 1.794$, $P = 0.111$) or groups ($F = 0.005$, $P = 0.942$), with no significant diet * group interaction ($F = 1.021$, $P = 0.418$); similarly, there was no significant effect of abrasive size ($F = 0.347$, $P = 0.708$), abrasive concentration ($F = 0.234$, $P = 0.630$), or groups ($F = 0.030$, $P = 0.864$),

Table 1
Composition of different pelleted diets fed to sheep (*Ovis aries*, n = 13) during a controlled dietary choice experiment.

Ingredients	Control	[4%] Small abrasives	[8%] Small abrasives	[4%] Medium abrasives	[8%] Medium abrasives	[4%] Large abrasives	[8%] Large abrasivesAAA
Lucerne flour (%)	71.15	71.15	71.15	71.15	71.15	71.15	71.15
Quartz dust[a] (%)	–	4	8	4	8	4	8
Beetroot molasses (%)	3	3	3	3	3	3	3
Mineral premix[b] (%)	2.8	2.8	2.8	2.8	2.8	2.8	2.8
Soybean oil (%)	2	2	2	2	2	2	2
Binding solution (%)	1.5	1.5	1.5	1.5	1.5	1.5	1.5
Monosodium phosphate (%)	0.6	0.6	0.6	0.6	0.6	0.6	0.6
Sodium bicarbonate (%)	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Dry matter (% as fed)	89	89	89	89	89	89	89
Nutrient composition (g/kg DM)							
Acid detergent fibre[c]	326	303	270	290	270	293	259
Acid detergent insoluble ash[d]	12	31	52	34	66	58	100
Ash	114	150	187	157	192	156	205

[a] Quartz dust was added to the diets at either [4%] or [8%], in different sizes depending on the diet: small, medium and large abrasives (mean particle size of 4 μm, 50 μm, and 130 μm respectively).
[b] Cu - controlled for sheep.
[c] ash corrected.
[d] a measure for abrasives content.

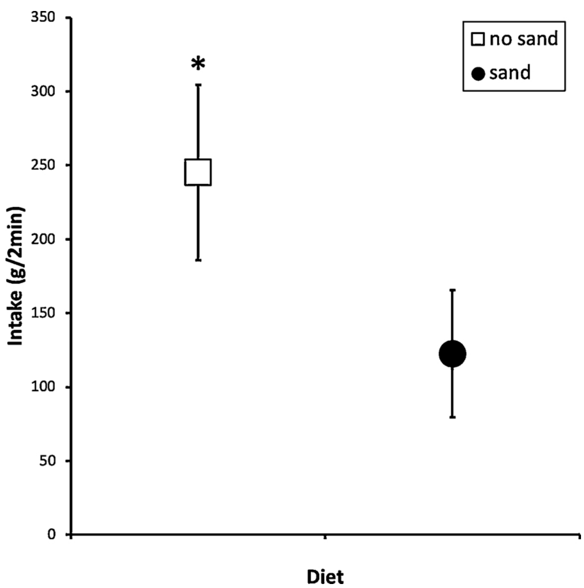

Fig. 1. Average intake of diets with and without added abrasives, fed to goats (*Capra aegagrus hircus*, n = 5) during a controlled dietary choice experiment. The animals were offered a diet containing added abrasives in the form of sand (mean size 233 μm) and a diet without added abrasives for two minutes. * Indicates significance ($P < 0.005$).

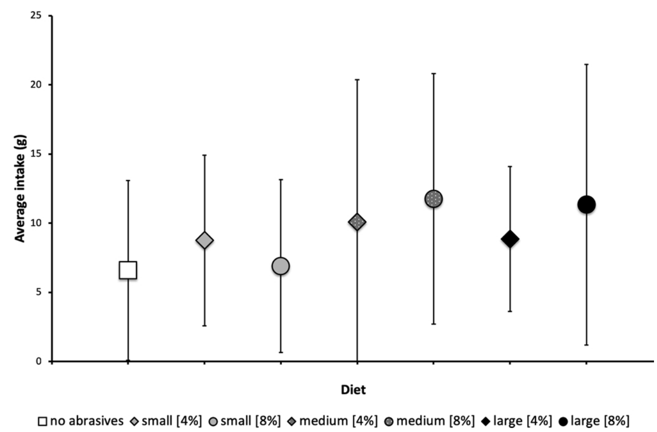

Fig. 2. Average intake of diets of varying abrasiveness, fed to sheep (*Ovis aries*, n = 13) during a controlled dietary choice experiment for ten minutes. Small, medium or large indicate the grain size of the abrasive added to the experimental diet in the form of silica dust (mean sizes: small 4 μm, medium 50 μm, and large 130 μm) and 8% or 4% indicate the concentration of added abrasives.

but the abrasive size * abrasive concentration interaction was again significant ($F = 5.259$, $P = 0.007$).

4. Discussion

Results show that the experimental goats favoured the diet without added sand. Although the goats had been accustomed to the GRS diet for months before the experiment, it is likely that the coarse, large-grained sand added to their diet created a perceptible sensation while chewing that the animals chose to avoid this diet. Anecdotally, a grinding noise was audible emanating from the masticating of the goats feeding on the GRS diet during the experiment. It should be noted that in studies where the same diets were fed to rabbits and guinea pigs, the addition of sand did not affect diet acceptance (Müller et al., 2014, 2015).

In the dietary experiment performed on sheep, results suggest no particular preference for any of the experimental diets. The silica particles used in this experiment were much smaller than those in the goat diets, suggesting that sheep may not be able to perceive contamination by dust during food intake. A study on sheep fed grass with manipulated silica rates (Massey et al., 2009) also showed no preference, the abrasives in question being phytoliths. The sheep studied by Healy and Ludwig (1965) had no other choice but to feed on highly eroded pastures, thereupon sustaining high amounts of tooth wear. Though ruminants display varying feeding strategies, one may question whether goats consciously avoiding grit is indicative of similar behaviour in other ruminant species and if so, to what extent ruminants can consciously avoid tooth wear when given the possibility.

Limiting factors to these experiments include the relatively small number of animals (goats n = 5, sheep n = 13) and the difference in experimental setup between studies. Although sheep and goats are not equivalent and do not represent all herbivores, we believe that the experimental results, which precluded an effect of novelty in sheep due to the repetitions the individuals were exposed to, provide insight into the different mechanisms of dietary selectiveness in regards to tooth wear. Furthermore, controlled feeding experiments are rare and an important baseline for better understanding animals' eating habits. A better representation of natural diets could have been achieved through forage-based diets, though this would have been impractical logistically and could have introduced other sources of bias. Using pelleted diets for the present study allowed the avoidance of differences in the total amount ingested, as the pellets were designed to be isocaloric and isonitrogenic.

In these diet preference trials, abrasive size averaged 233 µm in the goat diet and ranged from 4 to 150 µm in the sheep diet. In literature, abrasive sizes vary depending on location, (Kaiser et al., 2013; Strömberg, 2006) and can range from 5 to 250 µm and higher; specifically, grasslands show a range of 5–60 µm (mean diameter of 25 µm). Dust related to the Harmattan dust storm on the West African subcontinent blows particles from the Sahara Desert into the Gulf of Guinea and further. There, fine deposits were recorded as ranging between 20 and 40 µm with particles that travel long distances being smaller than 5 µm, while coarser dust raised by local disturbances in the same location ranged between 50 and 70 µm (McTainsh et al., 1997). If one were to generalise, abrasive particles could be separated into sand (62.5–2000 µm) and dust (< 20-70 µm), the latter more readily suspended by wind (Kok et al., 2012). Concerning plant-based abrasives, grass phytoliths - like those in the experimental goat diets - range from 10 to 50 µm, while lucerne contains no phytoliths, which is why it was used in the sheep diets. In the literature however, phytoliths cover a broad spectrum of sizes and can range from 5 to 250 µm (mean diameter of 25 µm for grasslands) (Strömberg, 2004). These are only some of the examples indicating the variability of abrasive sizes depending on context and location, and the near impossibility of categorising phytoliths, dust and grit sizes from every location in the world.

At precisely what size and/or concentration can animals start to detect abrasives, and what effect on tooth wear do these different sizes have? It has been suggested that various abrasives cause drastically different types of wear, with dust causing uniform wear without affecting the mesowear signal and large grit creating pathological wear at the other extreme (Kaiser et al., 2013), though this has yet to be tested experimentally. Volcanic ash is yet another example, as it is especially abrasive and is often reported to lead to excessive tooth wear in livestock (Flueck, 2016; Wilson et al., 2011). If dust is indeed imperceptible, evolutionary adaptations distinct from behaviour may be important in limiting the effects of its abrasion.

High-crowned, or hypsodont, teeth observed in grazers have evolved as a response to increasing wear related to the ingested material (dietary or otherwise), with morphological (Damuth and Janis, 2011; Janis and Fortelius, 1988; Mendoza and Palmqvist, 2008; Williams and Kay, 2001) and possible physiological (Dittmann et al., 2017) adaptations countering the detrimental effect of these abrasives. One physiological adaptation for wear compensation was recorded in goats and African buffaloes (*Syncerus caffer*), where increasing molar wear was correlated to small amounts of increasing root growth in the tooth cementum (Ackermans et al., 2019; Sanson et al., 2017). A further example of wear avoidance is the ruminant washing mechanism, a digestive function occurring when large grit ingested with plant matter is washed off by the liquid in the rumen before the material is regurgitated for rumination, thus reducing tooth wear. A more in-depth exploration of how different categories of external abrasives affect dietary preferences, as well as determining the point at which animals may no longer make a selection based on these abrasives, are interesting prospects that still require further investigation.

5. Conclusion

In this pilot study, goats ware shown to be capable of avoiding coarse grit in their diet, while sheep showed no preference for diets with no- or varying levels of finer abrasiveness. Though preliminary, these results provide insight on how these small ruminants detect external abrasives. These animals may select food motivated by the avoidance of tooth wear, but seemingly only up to a certain point at which abrasives are no longer detectable. Undetectable contamination could prompt more detrimental tooth wear when small abrasives are present in large quantities and either go unnoticed, or cannot be avoided.

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Competing statement

The authors declare no conflicts of interest.

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