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Seed dispersal capacity of sheep and goats in a near-coastal dry grassland habitat

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Abstract

Our aim was to investigate the influence of seed dispersal via sheep and goats on the biodiversity of the characteristic plant community and endangered plant species in near-coastal dry grasslands. We examined epi- and endozoochory by sheep and goats, grazing with a shepherd in a protected dry grassland area in northern Germany. We recorded the species and density of seeds trapped in fur and excreted in faeces of sheep and goats. These two ungulates dispersed seeds of 44% of all the species from the study site. These included seeds from 31 locally endangered plant species. The diversity and number of seeds were higher in fur and faeces of sheep compared to goats. This pattern was also found for the occurrence of seeds from plants characteristic to this habitat and Red List species. Extrapolation of these observations to the whole flock of sheep ($n = 630$) and goats ($n = 20$) suggests that there are about 357,000 seed transported in the fur whereas up to 1,500,000 seeds are dispersed via endozoochory. These observations underline the importance of free-ranging sheep and goats in shaping the biodiversity of plant species in dry grasslands.

Zusammenfassung

Ziel dieser Studie war es, die Bedeutung der Samenausbreitung durch Schafe und Ziegen auf die Biodiversität eines küstennahen Magerrasens zu untersuchen. Ein besonderer Fokus lag dabei auf den regionaltypischen Charakter- und Rote-Liste-Arten. Dazu wurde die epi- und endozoochore Samenausbreitung einer schäfergeführten Herde von Schafen und Ziegen auf einer geschützten Magerrasenfläche in Norddeutschland erforscht. Samen- und Artenzahl in Fell und Kot der Tiere wurden erfasst. Insgesamt repräsentierten 44% aller gefundenen Arten typische Charakterarten des Untersuchungsgebiets; 31 der gefundenen Arten stehen zudem auf der aktuellen Roten Liste des Landes Schleswig-Holstein in Deutschland. Im Vergleich zu den Ziegen, befand sich in Fell und Kot der Schafe eine signifikant höhere Samen- und Artenzahl. Gleiches gilt für die Häufigkeit von Charakter- und Rote-Liste-Arten. Hochgerechnet verbreitet die Herde, bestehend aus Schafen ($n = 630$) und Ziegen ($n = 20$), im Untersuchungsgebiet ca. 357.000 Samen im Fell und täglich ca. 1.500.000 über den Kot. Die Ergebnisse zeigen die besondere Bedeutung von Schafen und Ziegen für die Biodiversität von Charakter- und Rote-Liste-Pflanzenarten von Magerrasen auf.

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Keywords: Seed dispersal; Endozoochory; Epizoochory; Dry grasslands; Biodiversity; Large herbivores

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Introduction

Dry grasslands are important habitats for warm-adapted flora and fauna. These ecosystems have typically developed over centuries, and are largely used for low-intensity grazing. Typically this results in a high diversity of flora and fauna including a high frequency of locally endangered species and so they have high value for nature conservation (Poschlod & WallisDeVries 2002). For these types of sites, continued low intensity grazing is likely the best way to conserve existing biodiversity and more intensive agriculture or cessation of grazing is likely to be deleterious (Kahmen & Poschlod 2008; Bakker & Berendse 1999). Alternative management options such as mowing and mulching cannot maintain the typical pattern of disturbance necessary to sustain such semi-natural grasslands (Römermann, Bernhardt-Römermann, Kleyer, & Poschlod 2009) and grazing of large herbivores has proved to be a successful tool for maintenance of diversity (e.g. Bakker, De Bie, Dallinga, Tjaden, & De Vries 1983; Bouchard et al. 2003). Many studies have shown that livestock is an important vector for passive seed dispersal (e.g. Bruun & Fritzbøger 2002; Adriaens, Honnay, & Hermy 2007; Auffret, Schmucki, Reimark, & Cousins 2012), and grazing by sheep increased plant diversity by up to 30% in semi-natural meadows in Finland (Hellström et al. 2003). Accordingly, it is assumed that passive seed dispersal is an important factor for the maintenance of biodiversity.

Large vertebrate grazers can facilitate seed dispersal in two ways. Ingestion of seeds and their subsequent excretion in faeces is known as endozoochory. Seeds can also be trapped in the fur of vertebrates and dispersed, a process known as epizoochory. Endozoochory by large herbivores, especially ruminants, is a very efficient long-distance dispersal mechanism due to relatively long gut retention time and wide-ranging movements (e.g. Myers, Vellend, Gardescu, & Marks 2004; Manzano & Malo 2006; Ozinga et al. 2009). Herbivores may ingest a large number of seeds, partly because of their high nutritional value but also unintentionally. A variable number of viable seeds are excreted depending on their morphology and the processes in the gut (Pakeman 2001; Milotić & Hoffmann 2016). Epizoochory is facilitated by seed structures such as awns and hooks to enhance the possibility of being transported in the fur of the animals (Couvreur, Vandenbergh, Verheyen, & Hermy 2004). Furthermore, the length of time a seed stays attached to fur depends also on seed mass and the coat type of the animals (Tackenberg, Römermann, Thompson, & Poschlod 2006). Therefore, passive seed dispersal by large herbivores could support the ecological restoration of dry grassland plant communities depending on how many seeds are dispersed and over what distance.

Often sheep and goats are herded together because their feeding behaviours are complementary and goats can limit the establishment of trees by eating the seedlings. However the different feeding behaviours and fleece characteristics of sheep and goats might lead to differences in their impact

as seed dispersers. Therefore, the aim of our study was to investigate the differences between sheep and goats as seed dispersers in a dry near-coastal grassland habitat. In particular, the following questions shall be answered:

- Does the number and diversity of seeds dispersed by epizoochory and endozoochory differ between sheep and goats?
- Do epi- and endozoochorously dispersed seeds represent typical common local species and endangered species?

Materials and methods

The study was carried out in the near-coastal nature reserve “Dummersdorfer Ufer” near the city of Lübeck, federal state of Schleswig-Holstein, Germany (53°55' N, 10°5' E). The climate is humid suboceanic. Mean annual temperature is 8.8 °C (January: 1.0 °C; July: 17.7 °C) and mean precipitation is 712 mm year⁻¹ (German Meteorological Service). The reserve covers an area of 340 ha along a cliff coast of 5.5 km length. Dry grasslands, open slopes, sandy beach zones, natural forest and small wetland habitats are situated in the reserve. Our study area has a size of about 15 ha and comprises mainly dry grasslands (*Koelerio-Corynephoretea*, *Festuco-Brometea* and *Calluno-Ulicetea*) and, to a small extent, humid grassland (*Molinio-Arrhenatheretea*) (Benthien et al., unpublished). The area around the brackish coastal pond “Silkteich” comprising lagoon and salt meadow and was excluded from this study (see Appendix A: Fig. 1). Since 1996 the reserve “Dummersdorfer Ufer” has been grazed by semi-free ranging sheep (the local old domestic breed *grey horned heath sheep*) and cross-breed goats (*Boar goat* × *Valais blackthroat goat*). The flock grazes three times between April and October. These grazing events are relatively short and intensive (14–28 days, depending on the state of the vegetation); the flock is removed when the vegetation is thoroughly grazed. The flock, which is managed by a shepherd, consists of 630 sheep (400 females, 220 lambs, 10 males) and 20 adult goats (18 females, 2 males). Sampling took place on August 12th, 2013, after 72 h of grazing to ensure that faecal samples contained seed from local feeding only. August was chosen because most vascular plants carry fruits during that time of the year. Seeds were combed-out systematically from the fur of six adult female sheep and of six adult female goats to estimate epizoochoric seed transport. The sampling took place in the field. Sheep wool had grown to a length of 12–15 cm. Due to the cross breed, goats had smooth and straight hair all over their bodies. Most parts were short-haired with a fur length of 3–5 cm, except on upper parts of the legs and the belly, where the fur was 10–12 cm. The endozoochoric seed dispersal was assessed by collecting fresh faecal pellets from ten sheep and six goats. The faeces were dried in a standard drying oven to minimize fungal and bacterial growth (4 h at 120 °C, followed by 24 h at 50 °C). Dry weight was taken as reference value. The faecal samples were washed out through strainers with different mesh sizes

(1 mm, 0.8 mm and 0.5 mm) for 10 min. Then, the four fractions obtained were dried. Finally, the seeds were separated from remaining plant material using a binocular microscope. Seeds were identified using descriptions in Bojnanský and Fargasová (2007), Cappers, Bekker, and Jans (2006a), Jäger (2011) and Digital Seed Atlas (Cappers, Bekker, & Jans 2006b), Atlas of Seeds (Legagneux, Durhart, & Schricke 2013) and Seed Atlas (Radin 2013). Seed numbers were given as per gram dry faeces.

For epizoochorous seed dispersal, we divided all recovered seeds into five morphological types: (1) seeds with a smooth surface and no appendages, (2) seeds with a lightly structured, rough surface, (3) seeds with flat appendages (wings, wrinkles, cusps) or roughly structured surface, (4) seeds with straight elongated appendages (thorns, bristles, awns, long hairs) or (5) seeds with hook-shaped appendages. Additionally, a list of plant species of the study site was compiled, which comprised 137 vascular plant species. We identified 84 plant species (see Appendix A: Table 1) characteristic of the local dry and mesophilic grassland (hereafter called “characteristic species”). These plants were present and common in this plant community but absent from others and therefore indicative of the area. We classified all plant species which occur in the categories of the Red List of the Federal State of Schleswig-Holstein, Germany (Mierwald & Romahn 2006), as R (naturally extremely rare species of high ecological value), V (near threatened), 0 (extinct), 1 (critically endangered), 2 (endangered) or 3 (vulnerable).

Sheep and goats excrete small pellets about 10–15 times a day. Fresh sheep faeces contained about 50% (mean, $n = 10$) moisture and fresh goat faeces contained 46% (mean, $n = 6$) moisture. We extrapolated the amount of endozoochorously dispersed seeds to 100 g dry faeces.

We used the Jaccard similarity coefficient (Jaccard 1912) to evaluate the similarity between plant species derived from epi- and endozoochorous seed dispersal and character and Red List species by sheep or goats. Shapiro–Wilk and Smirnov tests were used to test deviation from normality. The Levene test was used to test for homogeneity of variances. Statistical testing for differences in seed dispersal between goats and sheep was done using F -tests for differences in variances and a two tailed t -test for differences in mean values, or Mann–Whitney U -test for differences in median. Aspects of seed morphology were tested for differences in sheep, goats and both, sheep and goats; we used the Welch test for differences in median followed by Dunnett post hoc test for multiple comparisons. All statistical analysis was done with PASW 18 (SPSS 2009).

Results

Epizoochory

We counted 4999 seeds from 67 plant species representing 15 plant families transported in the fur of ten sheep ($N = 3349$)

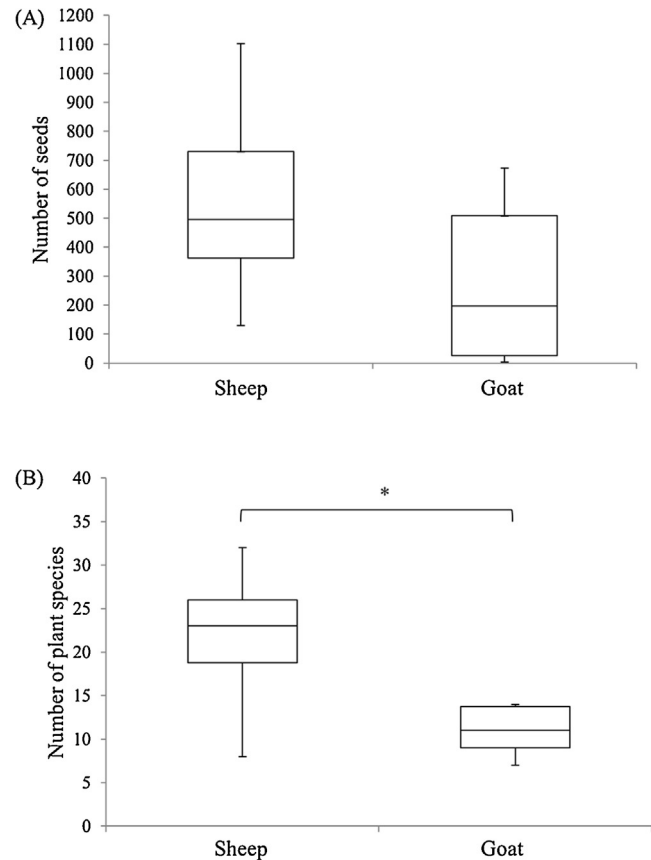


Fig. 1. Box and whiskers plots (min, Q_{25} , median, Q_{75} , max) compare results for sheep and goats in terms of (A) the total seed number counted in the fur; (B) the total number of plant species found in fur. Significant test results (two-tailed t -test for difference in means) are included in the graphics ($*p \leq 0.05$): $N_{\text{fur}} = 6$ for each species. For additional information, see Appendix Table 3.

and six goats ($N = 1650$). We found significant differences between sheep (63 plant species) and goats (22 plant species) in the number of plant species (total) and characteristic plant species as well as Red Listed species transported in the fur (Fig. 1 and Table 1). The most common species in the fur of sheep were *Urtica dioica* (29%), *Agrimonia eupatoria* (17%), *Arctium lappa* (16%) and *Holcus lanatus* (14%). Goat fur was dominated by two species: *Arctium lappa* (76%) and *Arctium minus* (14%). Plant species were similar with the exception of four species: *Cirsium vulgare*, *Galium odoratum*, *Lolium perenne* and *Myosotis stricta* which were found only in goat fur, although only as a single seed each.

The proportion of seeds found in the fur of sheep and goats differed clearly depending on the morphology of the seeds (Fig. 3). We found a positive correlation between seed morphology and the proportion of seeds transported in the fur of sheep and goats (sheep ($r_s = 3.54$, $p < 0.05$, $N = 1650$), goats ($r_s = 4.74$, $p < 0.05$, $N = 3349$), sheep and goats ($r_s = 4.47$, $p < 0.05$, $N = 4999$)), which suggests that seeds with more appendages, e.g. Type 5, are more frequently transported

Table 1. Differences in mean values of seed number (\pm standard error SE) in the fur and faeces of goats and sheep (M–W = Mann–Whitney–U-test).

	Sheep		Goat		Two-tailed <i>t</i>	M–W U/U(Tab)
	Mean	SE	Mean	SE		
Fur						
Character species	5.83	1.45	1.17	0.48	3.062*	
Red List species	2.83	0.70	1.00	0.45	2.200	
Faeces						
Character species	8.40	0.87	2.50	0.67	4.724*	
Red List species	5.10	0.81	0.67	0.33	5.067*	
Seeds/100 g DM	33.50	33.24	164.47	7.11		2/11*

* $p \leq 0.05$; Fur: $N = 6:6$ (sheep:goat); Faeces: $N = 10:6$ (sheep:goat).

in the fur, than those without, e.g. Type 1. The seed types that were transported most frequently were those with hook-shaped appendages (42%), seeds with straight, elongated appendages (22%) and seeds with a lightly structured, rough surface (31%). Seeds with a smooth surface and those lacking appendages (3%) as well as seeds with flat appendages (wings, wrinkles, cusps) or roughly structured surface (2%) constituted the smallest share of the transported seeds. Of the Red List species four out of a total of nine had no appendages (Type 1), with only one species present in the fur of goats (*Myosotis stricta*) and three in the fur of sheep (*Lotus corniculatus*, *Myosotis ramosissima*, *Thymus pulegoides*).

Endozoochory

We counted 919 seeds from 92 plant species representing 15 plant families transported in the faeces of sheep and goats. We recovered 694 seeds from 208 g dry faeces from 10 sheep and 225 seeds from 23 g dry faeces from six goats. This corresponds to 334 seeds per 100 g dry faeces of sheep and 978 seeds per 100 g dry faeces of goats. Our results suggest that sheep excreted a lower number of seeds per day than goats, while at the same time seeds from sheep faeces were from a significantly larger number of plant species (Fig. 2 and Table 1). Of the 14 plant families found in sheep faeces, *Poaceae*, *Cyperaceae*, *Fabaceae* and *Plantaginaceae* were the most frequent (see Appendix A: Table 2). In total, we counted 83 plant species representing 14 plant families in sheep faeces and 26 plant species representing 10 plant families in goat faeces.

We found *Urtica dioica* to be the most common seed in faeces of sheep (24%), followed by *Carex muricata* (12%), *Galium saxatile* (9%) and *Trifolium repens* (5%). *Urtica dioica* was also the most frequently recovered seed in goat faeces (36%), followed by *Carex hirta* (11%) and *Galium saxatile* (10%). *Calluna vulgaris*, *Glaux maritima*, *Rosa*

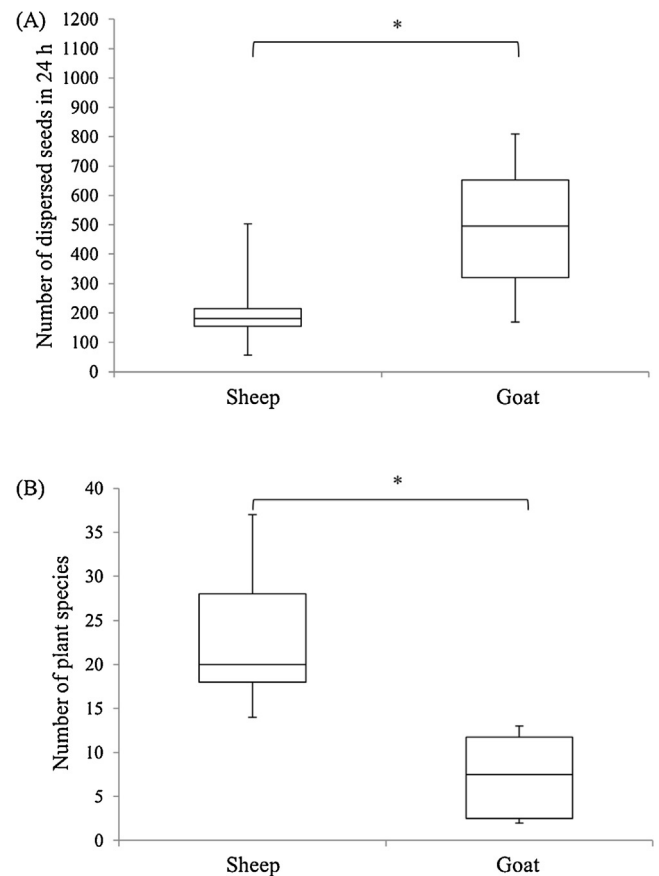


Fig. 2. Box and whiskers plots (min, Q_{25} , median, Q_{75} , max) compare results for sheep and goats in terms of (A) the total amount of daily dispersed seeds observed in faeces (the number of seed in faeces has been extrapolated to the daily amount of excreted faeces per individual); (B) the total number of plant species found in faeces. Significant test results (two-tailed *t*-test for difference in means) are included in the graphics (* $p \leq 0.05$): $N_{\text{faeces}} = 10$ (sheep), 6 (goats). For additional information, see Appendix Table 3.

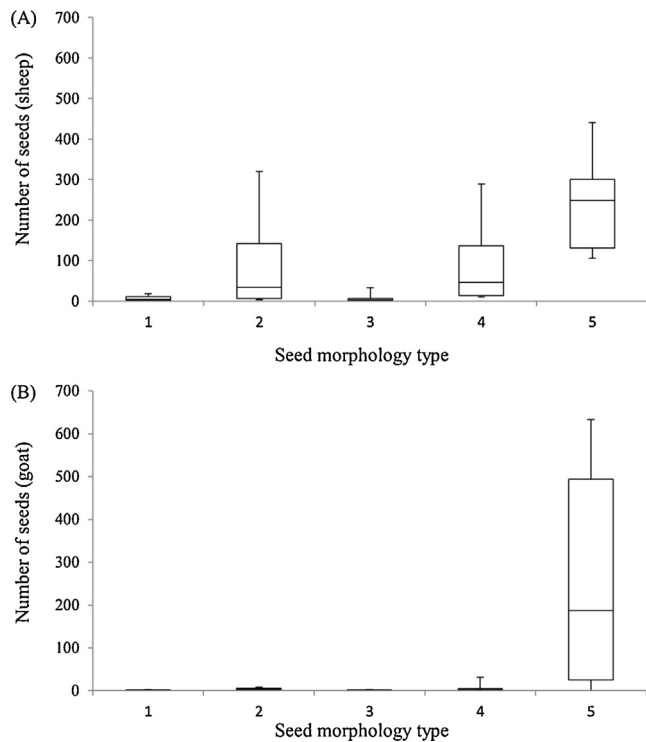


Fig. 3. Box and whiskers plots (min, Q_{25} , median, Q_{75} , max) show the abundance of different types of seed morphology observed in the fur of sheep (A) and goats (B). We divided all found seeds in five different morphological categories: seeds with a smooth surface and no appendages (1), seeds with a lightly structured, rough surface (2), seeds with flat appendages (wings, wrinkles, cusps) or roughly structured surface (3), seeds with straight elongated appendages (thorns, bristles, awns, long hairs) (4) or seeds with hook-shaped appendages (5). $N_{\text{sheep}} = 1650$, $N_{\text{goats}} = 3349$, $N_{\text{sum}} = 4999$.

agrestis, *Rosa cultivar*, *Rosa gallica*, *Rosa multiflora* and *Rosa sheradii* were found only in goat faeces.

Faeces vs. fur

We also tested for significant differences in the number of total plant species between faeces and fur (two-tailed *t*-test, $N_{\text{faeces}} = 16$, $N_{\text{fur}} = 12$). We found no significant difference in the abundance of characteristic and red-listed plant species ($p \leq 0.05$, $t_{\text{crit}} = 2.064$).

Overall, we found 38 characteristic plant species and 32 Red List species for Schleswig-Holstein, Germany (see Appendix A: Table 1). Sheep transported a significantly larger number of characteristic plant species in fur and faeces ($N_{\text{total}} = 45$) than goats ($N_{\text{total}} = 10$). We found the greatest similarity between the pool of characteristic species and those identified in sheep faeces ($J = 0.345$) and fur ($J = 0.190$). Goat fur ($J = 0.048$) and faeces ($J = 0.071$) showed a lesser similarity. In total, sheep also dispersed significantly more

red-listed plant species in fur and faeces ($N_{\text{total}} = 30$) than goats ($N_{\text{total}} = 5$).

The most common plants in fur and faeces belonged to the family *Poaceae*. They occurred considerably more often in the fur (see Appendix A: Table 2). In faecal samples, we found *Rosaceae* to be the second most frequent plant family while *Asteraceae* was the second most frequently occurring family in the fur. We made no comparisons of the number of seeds found in faeces and fur due to the lack of knowledge about the attachment time of seeds in fur.

Discussion

Our study demonstrated the importance of large herbivores in seed dispersal in dry grasslands, especially for characteristic and Red List plant species. This is significant for nature conservation and the maintenance of biodiversity.

Sheep and goats both had large numbers of seeds attached to their fur from a broad spectrum of plant species. As was expected in dry grasslands, most seeds were from *Poaceae*. However, the number and diversity of the seeds being dispersed differed strongly between sheep and goats largely due to differences in the length and structure of their fur. The rough, long, crimped wool of sheep carried a greater number and species diversity of seeds than the straight, smooth and mostly short hair of goats. For example, seeds of *Arctium*, which have pronounced hooks, were dominant in goat fur. Our results indicate that the seed morphology played an important role in the attachment of seeds to the fur of sheep and goats. The most frequently found plant species have anchor-like structures including hooks or awns. However there are two exceptions: *Urtica dioica* and *Agrostis capillaris*. A previous study made similar observations (Couvreur, Verheyen, & Hermy 2005). Both these species have small, light seeds, which are more easily attached and transported in fur (Tackenberg et al. 2006).

There was a strong difference in the number and species diversity of endozoochorously dispersed seeds between sheep and goats. Sheep fed mainly on grass and short roughage and as expected, sheep faeces most commonly contained seeds from the families *Cyperaceae* and *Poaceae*. However, we also found many *Rosaceae* seeds in sheep faeces. This was surprising because sheep do not normally eat shrubs and other woody vegetation. This could suggest that old domestic breeds like the *grey horned heath* are less sensitive to the negative impacts of plant secondary metabolites usually found in woody plants. As a consequence, these animals might not be typical grazers, but also browse on dicotyledonous plants, while other sheep breeds, like the merino sheep, which is used intensively for meat and wool production and bred to gain weight fast, typically graze on species with a low content of secondary plant metabolites, e.g. grasses. Goats browse more selectively than sheep

and can tolerate higher concentrations of plant secondary metabolites and higher concentrations of refractory materials such as lignin (Jason & Villalba 2006). Accordingly, we found seeds belonging to the plant family *Ericaceae* (*Calluna vulgaris*) in goat faeces but not in sheep faeces. Nonetheless, we found fewer seeds of shrubs and trees and a higher number of seeds from *Cyperaceae* in goat faeces than expected. The most frequently observed seeds in the faeces of both sheep and goats belonged to *Urtica dioica*. *Urtica dioica* is not common in the dry grasslands where the flock grazed. Other studies have made similar observations (Kuiters & Huiskes 2010). As *Urtica dioica* is known to be an indicator species for fertile nitrogen-rich soils, one explanation might be related to a higher protein concentration in these plants. Sheep and goats probably had access to *Urtica dioica* while they were being taken to their shelter during the night.

Endo- and epizoochorous seed dispersal is of great importance for the maintenance of biodiversity for both characteristic and endangered plant species in dry grassland communities. 44% of the listed characteristic species were found in the fur and faeces of sheep and goats. Furthermore, 42% of all observed plant species are red-listed by the federal state of Schleswig-Holstein with 22% categorized as endangered or threatened. In terms of epizoochorous seed dispersal the choice of breed might be of major importance for the dispersal of characteristic and endangered plant species. The long, crimped wool of the *grey horned heath* might better support long-distance dispersal and, hence, play an important role for the exchange of seeds between isolated dry grassland areas. In contrast, the straight, smooth hair of the mixed breed goats can be expected to support local seed dispersal due to a shorter attachment time of the seed. However, we have to take into consideration that fur structure is highly dependent on the breed. Therefore, we can find long and crimped fur also on some goat breeds like *Capra hircus laniger* as well as smooth, straight hair on sheep breeds like *Ovis orientalis musimon*. Old domestic breeds of sheep have been observed to be important dispersers in other studies, e.g. *Mergellan Sheep* (Kuiters & Huiskes 2010). Our study showed that the old domestic breed *grey horned heath* tends to feed on a broad spectrum of plant species. The diet of most modern sheep breeds might be different. However, from our data we cannot conclude if the choice of a specific sheep breed leads to the dispersal of more desirable plant species. Concerning this matter, studies about the differences in diet selection and seed dispersal between old and modern sheep breeds would be useful.

Seeds spend a longer time in the digestive system of ruminants compared to hindgut fermenters, leading to seed dispersal by defecation over greater distances. For the maintenance of biodiversity as well as the connection and exchange of isolated plant populations this might be a great benefit.

Further, our results showed that the mixed breed of *Boar goat* × *Valais blackthroat goat*, likewise, fed on a broader spectrum of plant species. As a management tool, goats are mainly used for keeping the landscape open by eating shrubs and small trees. This is why far fewer goats are grazed together with sheep.

Our study showed that goat faeces contained a considerable amount of local characteristic and Red List plant species. This indicates that the role of goats for the maintenance of biodiversity in dry grassland habitats might be underestimated. A study in a lowland dry grassland indicated that many grassland species germinated from herbivore faeces (Pakeman 2001). Additionally, small seed size was shown in another study to be an important characteristic of seeds that survive ingestion and gut passage (Pakeman, Digneffe, & Small 2002). These species germinated from the dung in heathland and dune slack vegetation, while large or elongated seeds did not. Our finding of many small seeds in the faeces of sheep and goats indicates that most seeds might be able to germinate but specific data are needed.

We assume in this study that a sheep excretes 665 g and a goat 300 g dry faeces per day (Eichberg & Wessels-de Wit 2011; Soumaré 1981). On a daily basis, the extrapolated number of endozoochorous dispersed seeds amounts to 1,458,314, with 1,398,600 seeds carried by 630 sheep and 59,714 seeds by 20 goats. Seeds transported in the coats of the flock grazing in the study area sums up to about 357,040.

Conclusion

Our study showed that sheep and goats are important dispersal vectors for a broad spectrum of plant species. We conclude that endo- and epizoochorous seed dispersal is of great importance for the maintenance of biodiversity, especially for characteristic and endangered plant species in semi-natural dry grassland communities. Additionally, decisions about which large herbivores to use will influence the final outcome. Goats differ not only in fur structure, but also in food selection. Even though the main reason for grazing goats in the larger flock of sheep is to suppress the growth of shrubs and trees, they also provide numerous benefits for the local vegetation. This might also hold true for the feeding behaviour and seed dispersal properties of the old sheep breed *grey horned heath* especially for their influence in the maintenance of plant biodiversity.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2016.03.006>.

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