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Short communication

The role of domestic herbivores in endozoochorous plant dispersal in the arid Knersvlakte, South Africa

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Abstract

Herbivores can act as dispersal vectors by purposely or accidentally ingesting ripe fruits, and thus endozoochory is one determining factor for plant distribution patterns. The objective of our study was to investigate to what extent plants of major taxonomic groups of the Knersvlakte (Succulent Karoo, South Africa) are endozoochorously dispersed. On three different farms in the central Knersvlakte, dung of domestic herbivores was collected and analysed by the seedling-emergence method. The resulting species composition was compared to the standing vegetation of thirty-four 1000-m² plots each recorded on one hundred 400-cm² subplots. Our results show that domestic livestock facilitated the dispersal of taxa characteristic of the Knersvlakte, in particular Aizoaceae. Among the taxa of this family, the local endemic dwarf shrub *Drosanthemum schoenlandianum* emerged with the highest frequency in dung (14.5% of all seedlings). For the Asteraceae, which are frequent in the standing vegetation of the Knersvlakte, however, endozoochorous dispersal by livestock was only of minor importance. Conservation planning should consider these dispersal patterns on behalf of future population dynamics. The complete exclusion of livestock might change current processes and thus alter vegetation patterns.

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1. Introduction

Large herbivores influence vegetation in diverse ways. Besides processes related to disturbance, e.g. compositional shifts or changes in diversity, herbivores can affect vegetation by driving dispersal patterns of plant species via zoochory (Fenner and Thompson, 2005). One means of animal-induced dispersal is the fruit consumption followed by passing of viable seeds in dung (Fenner and Thompson, 2005).

The germination success of seedlings from dung is determined by three main factors. First, the seeds have to be eaten by an animal. This can happen either deliberately due to high palatability or accidentally when a herbivore consumes seeds along with palatable leaves or neighbouring palatable plants ('foliage is the fruit', Janzen, 1984; Pakeman et al., 2002).

Second, the seeds have to survive the digestive system (Cosyns et al., 2005). Third, depending on the species, dormancy may need to be broken, and germination requirements have to be fulfilled (Malo, 2000).

The Knersvlakte in South Africa is known for its distinct flora that is outstandingly diverse and endemic-rich, in particular for an arid region (Hilton-Taylor, 1996; Van Wyk and Smith, 2001). Thus it has been recognised as one of the highest conservation priority areas of the country (Desmet et al., 1999; Hilton-Taylor and Le Roux, 1989). The conservation management authority of the Western Cape Province, Cape-Nature, is now in the process of establishing a conservation area in the region. Decisions must be made regarding future land-use management in the conservation area, including enclosure or enclosure of domestic livestock.

The Knersvlakte has been subjected to grazing by domestic livestock for about 2000 years (Boonzaier et al., 2000). Before the first European settlement about 150 years ago, Khoikhoi pastoralists practiced transhumance throughout the region. In addition, high numbers of wild ungulates (e.g. antelopes) used

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to freely roam the country. They have been drastically reduced in numbers since the intensification of livestock farming (Hoffman and Rohde, 2007). The floristic composition of the Knersvlakte today, with its high percentage of endemic plant species, has assumingly been partly shaped by herbivory (Desmet, 2007). But how do herbivores influence the vegetation patterns and population dynamics? Are the plants of the Knersvlakte endozoochorously dispersed?

As to date no study about endozoochory by large mammals has been conducted in the Knersvlakte or anywhere else in Namaqualand, knowledge about the role of herbivores in the dispersal of vascular plant species of this area is scarce, especially as concerns endemics. The geographically closest studies on endozoochorous dispersal have been carried out in the Southern Karoo by Milton (1992) and Milton and Dean (2001) and in the Cape Floristic Region by Shiponeni and Milton (2006).

The objective of this study is to investigate the contribution of domestic herbivores in the endozoochorous dispersal of Knersvlakte plant species. Our study deals with current processes and therefore contributes to the development of models predicting future vegetation patterns. We aim at obtaining initial insights into the general feasibility of a more comprehensive study in this area and at providing basic understanding of processes that could be crucial for the continued existence of this diverse and endemic-rich region of highest conservation priority.

2. Methods

2.1. Study area

The Knersvlakte (30°27'–32°05' S, 17°46'–19°06' E) is an extensive penneplain that forms the southern tip of the Namaqualand and is part of the Succulent Karoo Biome. According to Myers et al. (2000), the Succulent Karoo is the only arid example among 25 internationally recognised global biodiversity hotspots. The Knersvlakte hosts more than 150 endemic vascular plant species (Van Wyk and Smith, 2001), and is often referred to as a centre of endemism and diversity (Hilton-Taylor, 1996; Jürgens, 1997; Van Wyk and Smith, 2001).

The semi-arid climate is characterised by a relatively predictable winter rainfall with an average of 116 mm annually (mainly falling in May–August), occasionally supplemented by fog and dew (Mucina et al., 2006). Temperatures range from 5–10 °C in winter to 30–35 °C in summer (Mucina et al., 2006).

One special characteristic of the Knersvlakte is the frequent occurrence of quartz fields with dense cover (sometimes 100%) of gravel-sized quartz particles. This quartz gravel is derived from weathered quartz veins running through parental material of limestone, shale and phyllites (Schmiedel and Jürgens, 1999). These conditions create a unique habitat with a distinct flora dominated by succulent dwarf shrubs, mainly Aizoaceae (Schmiedel and Jürgens, 2004).

2.2. Sampling

The sampling was carried out from early August through early November 2007 on three farms in the central Knersvlakte. In total,

34 plots were established, on one farm with 17 plots (moderately grazed, 17 ha per Small Stock Unit = SSU, after Esler et al., 2006), one farm with 8 and one with 9 plots (both more intensively grazed, 11 ha per SSU). The plots measured 20 m × 50 m and contained 100 subplots 20 cm × 20 cm in size. All juvenile and adult individual plants rooting in the subplots were identified (for details, see Haarmeyer et al., 2010). Nomenclature follows Germishuizen and Meyer (2003) except for the Aizoaceae which were classified according to Hartmann (2002). On 29 of the 1000-m² plots and their immediately adjacent areas, dung (old and fresh, one mixed sample of 2–60 g per plot) of domestic herbivores (sheep or goats, determination according to Stuart and Stuart, 2000) was collected according to availability. On the remaining five plots, we did not find any dung of domestic herbivores.

In June 2008, the dung samples were suspended overnight in tap water (10 g of dry dung per sample in 50 ml water, or less according to the sampled mass). The next day, the moist dung was applied onto a sterilised sand/peat mixture (1:1 volume ratio) in plant pots (10 cm × 10 cm × 10 cm) in the greenhouse of the University of Hamburg, Germany. The greenhouse temperature fluctuated between about 15 and 30 °C (maximum: 50 °C) daily, which approximates diurnal temperature variation in the field plots. For six weeks, the emerging seedlings were identified and counted twice a week until the number of additionally germinated seedlings was less than 1% of the total number emerged up to that point. All individuals were identified as far as possible (species, genus or family) or else classified into one of the following morphologically distinguishable groups ('morpho-types'): 'mesemb' (i.e., Aizoaceae subfamilies Ruschioideae or Mesembryanthemoideae sensu Hartmann, 2002), 'unidentified dicots', and 'unidentified geophytic monocots'.

For the analyses, we used descriptive methods and, due to the explorative nature of the sampling, refrained from carrying out inferential statistics. We compared the percentage of seedling numbers for the different families and morpho-types of the dung samples with those of the standing vegetation in plots of the same grazing intensity. All three farms are situated in the same vegetation type (SKk 2: Central Knersvlakte Vygieveld and SKk 3: Knersvlakte Quartz Vygieveld; Mucina et al., 2006) and can therefore be regarded as similar. However, as another study has shown that the vegetation differs between moderately and intensively grazed areas (Haarmeyer et al., in press), we analysed them separately.

3. Results

Altogether, 1.528 kg of dung (moderate: 0.738 kg; intensive: 0.790 kg) was sampled, from which the seedlings began to emerge on the fourth day after the dung was watered. By the sixth day, two thirds of the seedlings had already germinated, and after 28 days, 97% had emerged. From the 29 samples of domestic animal dung, altogether 909 seedlings (595 seedlings/kg) germinated (moderate grazing: 736 with 932 seedlings/kg; intensive grazing: 173 seedlings with 234 seedlings/kg) with a mean of 31.3 ± 53.1 SD seedlings per sample (range 0–213).

Table 1

List of taxa germinated from domestic herbivore dung and their abundances and percentage of the total number of individuals; asterisks indicate species not found in the standing vegetation in the plots.

Species	Number of seedlings	Percentage of total (%)
Aizoaceae: Mesembs		
* <i>Antimima dualis</i> (N.E.Br) N.E.Br	1	0.1
<i>Antimima</i> spec.	4	0.4
<i>Antimima watermeyeri</i> (L.Bolus) H.E.K. Hartmann	4	0.4
<i>Aridaria serotina</i> L.Bolus	5	0.6
<i>Caulipsolon rapaceum</i> (Jacq.) Klak	11	1.2
<i>Cephalophyllum framesii</i> L.Bolus	6	0.7
<i>Drosanthemum deciduum</i> H.E.K. Hartmann & Bruckmann	4	0.4
<i>Drosanthemum diversifolium</i> L. Bolus	1	0.1
<i>Drosanthemum globosum</i> L. Bolus	8	0.9
<i>Drosanthemum ramosissimum</i> (Schltr.) L. Bolus	1	0.1
<i>Drosanthemum</i> spec. ('glossy')	14	1.5
<i>Drosanthemum schoenlandianum</i> (Schltr.) L. Bolus	132	14.5
<i>Drosanthemum</i> spec.	7	0.8
<i>Malephora purpureo-crocea</i> (Haw.) Schwantes	36	4.0
Mesemb spec.	361	39.7
<i>Mesembryanthemum nodiflorum</i> L.	1	0.1
<i>Phyllobolus nitidus</i> (Haw.) Gerbaulet	2	0.2
<i>Psilocaulon</i> spec.	1	0.1
<i>Ruschia</i> spec.	17	1.9
Aizoaceae: Non-mesembs		
* <i>Galenia africana</i> L.	1	0.1
* <i>Galenia fruticosa</i> (L.f.) Sond.	19	2.1
<i>Galenia</i> spec.	2	0.2
<i>Tetragonia fruticosa</i> L.	3	0.3
<i>Tetragonia microptera</i> Fenzl	11	1.2
<i>Tetragonia</i> spec.	2	0.2
Asteraceae		
<i>Amellus microglossus</i> DC.	5	0.6
Asteraceae spec.	1	0.1
Asteraceae spec. 1 ('succulent')	1	0.1
<i>Foveolina dichotoma</i> (Thell.) Källersjö	6	0.7
<i>Oncosiphon suffruticosum</i> (L.) Källersjö	3	0.3
<i>Osteospermum pinnatum</i> (Thunb.) Norl.	1	0.1
<i>Rhynchosidium pumilum</i> (L.f.) DC.	1	0.1
Brassicaceae		
* <i>Lepidium desertorum</i> Eckl. & Zeyh.	12	1.3
Caryophyllaceae		
Caryophyllaceae spec.	3	0.3
<i>Spergularia media</i> (L.) C. Presl. ex Griseb.	1	0.1
Chenopodiaceae		
<i>Atriplex lindley</i> subsp. <i>inflata</i> (F.Muell.) Paul G. Wilson	1	0.1
<i>Atriplex semibaccata</i> var. <i>typica</i> Aellen	13	1.4
<i>Atriplex</i> spec.	1	0.1
<i>Chenopodium album</i> L.	14	1.5
<i>Chenopodium</i> spec.	39	4.3
<i>Salsola</i> spec.	1	0.1
Fabaceae		
Fabaceae spec.	9	1.0
Poaceae		
* <i>Fingerhuthia africana</i> Lehm.	1	0.1
Poaceae spec.	14	1.5
Scrophulariaceae		
Scrophyllariaceae spec.	1	0.1
Solanaceae		
* <i>Lycium</i> spec.	3	0.3

Table 1 (continued)

Species	Number of seedlings	Percentage of total (%)
Unidentified geophytic monocots	2	0.2
Unidentified dicots	117	13.4
Total number of seedlings	909	
Mass of dung [kg]	1.528	
Seedlings per kg dung	595	

We distinguished 46 taxa (at the species, genus or family level) from nine families; the remaining seedlings could be assigned to the morpho-types 'unidentified dicots', and 'unidentified geophytic monocots'. For a complete list of taxa and their seedling abundances, see Table 1.

In the standing vegetation, we found a total of 7057 individual plants of 152 species or taxonomic entities (moderate grazing: 105 species, intensive grazing: 124 species) of which the majority were Asteraceae and Aizoaceae. The most frequent species was the annual herb *Foveolina dichotoma*. The ten most abundant species of the standing vegetation of the two grazing intensities are listed in Table 2. A comparative overview of the most abundant families and morpho-types among both the standing vegetation and the dung-germinated seedlings is given in Fig. 1.

The spectrum of the endozoochorously dispersed flora resembled the species composition of the standing vegetation in the plots. In both cases, the mesembs were dominant. However, though this was the most frequent taxon among the seedlings emerging from dung of domestic herbivores (>64% of all seedlings) as well as in the standing vegetation of the moderately grazed plots (51%), it was only second (22%) in the standing vegetation of the intensively grazed plots (see Fig. 1). The high abundance of the endemic *Drosanthemum schoenlandianum* in the dung compares well with its relatively high abundance (3.4% of all individuals, among 152 recorded species in total) in the standing vegetation (moderate and intensive grazing).

The Asteraceae, although represented in the endozoochorous flora by seven different identified taxa, were less frequent among the dung-germinated seedlings (2%) than in the recorded standing vegetation, where they constituted 50% of all individuals (60% on intensively and 32% on moderately grazed plots). Poaceae, Fabaceae, Brassicaceae, and Chenopodiaceae were abundant families among both dung-germinated seedlings and standing vegetation, although the proportion of Chenopodiaceae was clearly higher (8%) among seedlings compared to the standing vegetation (1%). Crassulaceae and Oxalidaceae, though abundant in the standing vegetation, did not emerge at all from dung.

4. Discussion

The high abundance of mesemb seedlings emerging from domestic animal dung indicates a relatively high importance of endozoochory by domestic livestock for the dispersal of some species of this group. In particular, the endemic *D. schoenlandianum* emerged in high number from dung and can therefore

Table 2

The ten most abundant species of the standing vegetation in plots, their families, abundances and percentage of all 7057 individuals on 3400 subplots of 0.04 m² (i.e. a total area of 136 m²).

Species	Family	Number of individuals	Percentage of total (%)
<i>Foveolina dichotoma</i> (Thell.) Källersjö	Asteraceae	1184	16.8
<i>Rhynchosidium pumilum</i> (L.f.) DC.	Asteraceae	806	11.4
<i>Helichrysum alsinoides</i> DC.	Asteraceae	478	6.8
<i>Drosanthemum diversifolium</i> L. Bolus	Aizoaceae	299	4.2
<i>Cephalophyllum spissum</i> H.E.K. Hartmann	Aizoaceae	288	4.1
<i>Drosanthemum schoenlandianum</i> (L.f.) (Schltr.) L. Bolus	Aizoaceae	240	3.4
<i>Oncosiphon suffruticosum</i> (L.) Källersjö	Asteraceae	220	3.1
<i>Karoochloa schismoides</i> (Stapf ex Conert) Conert & Türpe	Poaceae	202	2.9
<i>Amellus microglossus</i> D.C.	Asteraceae	188	2.7
<i>Oxalis</i> spec. ("small leaves")	Oxalidaceae	184	2.6

be expected to be palatable. Mesembs usually show short-distance ombrohydrochorous dispersal (Parolin, 2006), a specific adaptation to abiotic environmental conditions like fine-scale habitat variation (Ellis and Weis, 2006) and intra-annual rainfall patterns (Parolin, 2006). However, in contrast to short-distance ombrohydrochory, domestic animals, such as sheep and goats, can carry seeds as far as they travel in 24–36 h, which is about the retention time for the digestive system of

sheep (Huston et al., 1986). According to Samuels et al. (2007) this time period would correspond to a maximum distance of 3–17 km. Domestic animals can thus promote long-distance dispersal in mesembs, which previously had been attributed to the action of strong winds or water (Ihlenfeldt, 1994).

The predictably low abundance of the usually anemochorous Asteraceae among the seedlings indicates a minor importance of endozoochory for their dispersal. As the family was not completely absent from the emerged seedlings, obviously, seeds of at least some of its species seem to be capable of surviving the digestive system of ungulates. Hence it can be suggested that either the species of this family were hardly palatable or that the seeds remained dormant after surviving ingestion and gut passage. Moreover, many Asteraceae species shed their fruits when ripe, which reduces the possibility of being browsed by an animal.

The complete absence of Crassulaceae species is probably due to their unpalatability, characteristic of many members of this family (Kellerman et al. 1996).

In comparison to the only other study concerning endozoochorous mammalian dispersal conducted in the Karoo (Succulent–Nama Karoo interface, Milton and Dean, 2001), the present study yielded on average almost four times as many seedlings per kilogram of dung.

In this context it is also remarkable that there were four times more seedlings under moderate compared to intensive grazing which could be one explanation for the differences in seedling yield between different studies discussed above.

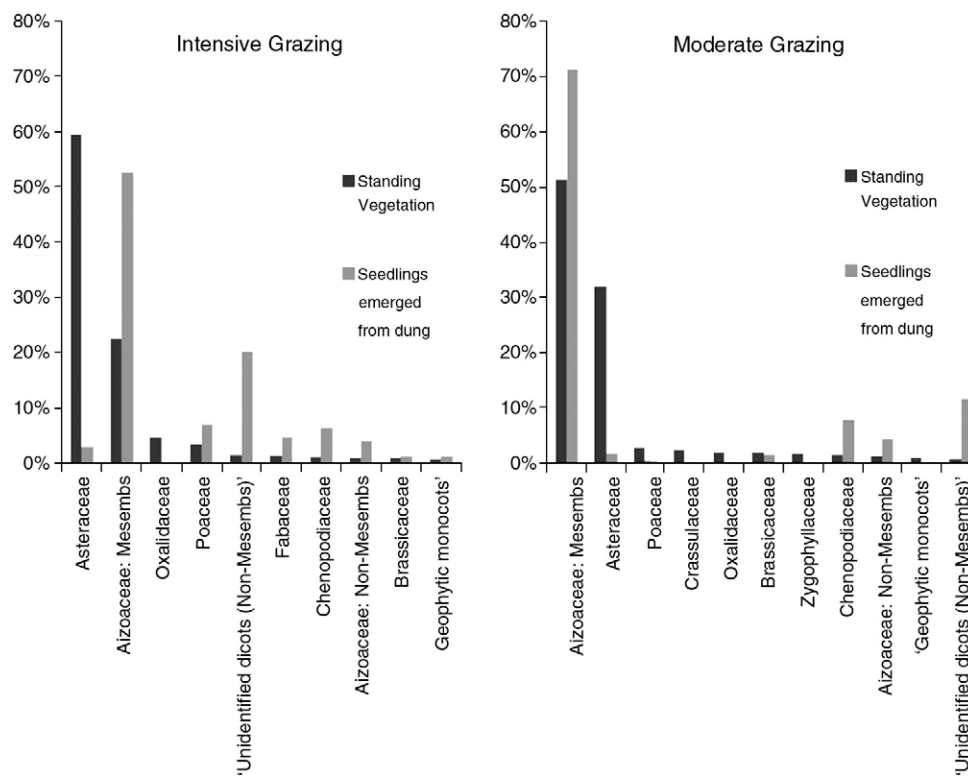


Fig. 1. Percentage of individuals of different families and morpho-types emerging from domestic herbivore dung compared to that in the standing vegetation for moderately grazed (left) and intensively grazed (right) plots. The percentage values relate to the relative abundance of seedlings within the respective category (dung or standing vegetation). Only families with percentages >1% in at least one of the intensities are shown. The notation 'mesembs' refers to the subfamilies Mesembryanthemoideae and Ruschioideae of the family Aizoaceae; 'Aizoaceae: non-mesembs' refers to the subfamilies Aizoideae and Tetragnonioideae.

In accordance to our study, Milton and Dean (2001) also found that mesembs constituted a large portion of the individuals emerging from dung. The Chenopodiaceae, which were rather numerous in the dung of domestic livestock in our study, were of only minor importance in the above-mentioned study. Grasses (Poaceae), on the other hand, germinated much more frequently from the dung sampled in the study of Milton and Dean (2001) compared to our study. As grasses generally occur infrequently throughout the Knervlakte, due to a combination of low rainfall and fine-textured soils (Esler et al., 2006), this result is not surprising.

Our results and those of Milton and Dean (2001) agree in the importance of domestic livestock for the dispersal of Aizoaceae in general and mesembs in particular, while we found a much higher incidence of endozoochorous dispersal in Chenopodiaceae. It can be concluded that domestic livestock facilitates the dispersal of characteristic taxa of the vegetation of today's Knervlakte, in particular Aizoaceae, and thus, in addition to strong winds, helps the primarily short-distance dispersed mesembs to occasionally disperse across long distances. In contrast, the dispersal of Asteraceae does not seem to be promoted by grazing itself. It would be interesting, though, to examine how the results may differ when additionally considering epizoochorous dispersal. Generally, the role of domestic herbivores in species dispersal should not be underestimated. In the past 2000 years its effects may have led to the current species composition and their functional traits. Conservation planning should take into account this dispersal potential. The complete exclusion of livestock might change current processes and thus alter vegetation patterns. The positive effects of grazing should be weighed against potential negative impacts (e.g. compositional shift and loss of diversity and biomass).

Further studies should aim at quantifying the demonstrated effects of endozoochory, especially with regard to differences between domestic stock and wild herbivores, by systematically sampling dung of different herbivores across a larger area over a longer period. Models predicting future vegetation patterns e.g. for the purpose of conservation management, should take into account the importance of domestic herbivores for the dispersal of plant species as well as potential differences in the endozoochory by wild herbivores.

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