

Complementarity of epi- and endozoochory of plant seeds by free ranging donkeys

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Epizoochory and endozoochory are well-recognized long-distance seed dispersal mechanisms, yet their relative importance has hardly been studied before. Here, epi- and endozoochory were compared on donkeys foraging in a species-rich 100 ha coastal dune ecosystem, through *in vitro* germination of zoochorous material obtained by fur brushing and dung collection. We identified 6675 seedlings of 66 plant species, covering 20% of the species recorded in the study area. Of the 66 species, only 16 occurred in both epi- and endozoochory samples, demonstrating the complementarity of both dispersal mechanisms. The species composition in the zoochory samples reflected a strong seasonality, and seedling numbers were partly correlated with species abundance in the study area. The non-zoochorously dispersed species in the study area differed from the zoochorous species in seed size and weight, plant height, life span, dispersal strategy and seedbank persistence. Dispersal-relevant plant traits were used to derive dispersal-functional plant types for all species in the study area. Epizoochory showed to be more specific than endozoochory and was associated with a more narrow range of dispersal-functional plant types.

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Long-distance seed dispersal mechanisms have recently received much attention, especially in the context of understanding and predicting plant migration (Cain et al. 1998, Clark et al. 1998, Higgins and Richardson 1999, Pakeman 2001). The relevance of seed dispersal research has become increasingly clear given the problem of plant invasions, limited dispersal in fragmented habitats (Poschlod and Bonn 1998, Higgins et al. 2003), and the necessary plant migrations in response to global change (Watkinson and Gill 2002). Also the insight that seed limitation is a major ecological constraint in several ecosystems (Turnbull et al. 2000, Zobel et al. 2000, Dalling et al. 2002, Foster and Tilman

2003, Verheyen et al. 2003) has orientated research efforts towards dispersal.

Zoochory, the external and internal dispersal of plant seeds by animals, is an important dispersal mechanism. Epizoochory, on the one hand, is mainly associated with adhesive seed adaptations facilitating attachment to mammalian fur, although also species adapted to other dispersal modes or without obvious adaptations disperse epizoochorously (Fischer et al. 1996, Heinken and Raudnitschka 2002, Couvreur et al. 2004a, b, c). Endozoochory, on the other hand, covers the consumption of fleshy fruits by frugivores (Debussche and Isenmann 1989, Amico and Aizen 2000, Tabarelli and

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Peres 2003) and the consumption of seeds of grasses and herbs by herbivorous mammals (Janzen 1984, Welch 1985, Gardener et al. 1993, Malo and Suárez 1995b, Pakeman et al. 1998, Heinken et al. 2001, Cosyns 2004, Cosyns et al. 2004). Edible vegetative plant parts (Janzen 1984) and seed resistance to digestion (Pakeman et al. 2002) are hypothesized to be adaptations to endozoochory by large herbivores.

Both epi- and endozoochory are key factors determining plant distribution (Welch 1985, Malo and Suárez 1995a, Fischer et al. 1996, Poschlod and Bonn 1998, Pakeman et al. 2002). Moreover, they may provide a means of “directed dispersal” for many species relying on disturbed habitats, which are frequented and even generated by herbivores through feeding, trampling or wallowing (Janzen 1984, Wenny 2001).

Recently, an increasing number of attempts to model zoochorous dispersal has been undertaken (Pakeman 2001, Higgins et al. 2003, Vellend et al. 2003). Yet, basic and reliable knowledge of which plants are dispersed zoochorously and which factors and plant traits direct zoochorous dispersal is still very limited. Several authors have therefore explicitly stressed the need for more data on the influencing factors of zoochory (Higgins and Richardson 1999, Bullock et al. 2002, Levin et al. 2003). Studies which fill this gap are scarce, especially comparative studies of epi- and endozoochorous dispersal. Both mechanisms have been studied simultaneously on sheep in calcareous grasslands (Fischer et al. 1995), on Galloway cattle in moorland pastures (Stender et al. 1997), and on wild boar and roe deer in a forest ecosystem (Heinken et al. 2002). However, the additive and/or complementary effects of epi- and endozoochory, as well as the role of dispersal-functional plant traits in facilitating epi- or endozoochory, remain largely unexplored.

In this paper, we compare epi- and endozoochorous seed dispersal by donkeys grazing in a species-rich coastal dune ecosystem. We test the following specific research hypotheses: 1) Different plant species are dispersed by epi- and endozoochory. 2) The species abundance in the study area influences the species abundance in the zoochory samples. 3) Morphological and ecological plant traits relevant for dispersal differ between species dispersed by zoochory and species not dispersed by zoochory.

Material and methods

Study area

The study was carried out in the coastal dune nature reserve “Houtsaegerduinen” (100 ha), in the west of Flanders, Belgium (51°05'N, 2°35'E). The variation in abiotic conditions and the historical land use in this coastal dune system led to a high plant species

richness and a wide range of plant communities. Although the dune landscape is dominated by *Hippophae rhamnoides* and *Ligustrum vulgare* shrubs, grassland covers at least one third of the area. Part of the grassland is scattered within the scrub as small and mostly species poor remnants of dune grassland or as species poor *Calamagrostis epigejos*–*Arrhenatherum elatius* dominated patches, which established after scrub degradation. Flowering and fruiting of the plant species is concentrated from April to October. Six donkeys were released in the study area in 1997 for nature management purposes; the herd counted 15 animals at the time of data collection.

Data collection and treatment

The zoochory samples were collected in four different time periods between June and October 2000: early summer (9 June–19 July), mid-summer (20 July–19 August), late summer (20 August–19 September) and early autumn (20 September–19 October). In the case of epizoochory, 41 samples were collected. Respectively 8, 11, 15 and 7 donkeys were sampled in each of the four time periods, by brushing the entire fur of each individual with a very fine horse brush during 15 min. In the case of endozoochory, the number of sampled donkeys was 4 in early summer, and 8 in each of the three other periods. For practical reasons, the dung of two donkeys was pooled to one sample with a volume of 2.5 l, resulting in 28 sampled donkeys, pooled in 14 samples. Freshly deposited excrements were used, hereby avoiding the lowermost dung part to prevent contamination with seeds of underlying plants or from the soil seedbank.

In the laboratory, the samples were prepared for the seedling emergence method (Roberts 1981, Ter Heerd 1996). The excess of hair was carefully removed from the dry epizoochory samples, while the endozoochory samples were air-dried in a greenhouse, then stored for two weeks at 4°C (without imbibition of the seeds), and subsequently softly homogenized in a Retsch mill (type SK 100) to allow easy spreading. All samples were sown in trays with sterilized potting soil, and kept in laboratory conditions with a daily light-exposure of 16 h, daily watering and occasional soil disturbance in order to light-expose buried seeds. During six months, species and seedlings were recorded, and immediately removed to prevent competition and flowering. Unrecognizable seedlings were grown separately until identification was possible. After six months, the epizoochory samples were stratified for 2 months at 4°C in imbibed conditions, after which the germination cycle was prolonged for another three months. However, no new species emerged during this second germination period.

The abundance of all plant species in the study area was recorded on several occasions between 1990 and 2000, using Tansley scaled ordinal abundance estimates for all species in the entire study area, in combination with percentage cover estimates in 1 m² quadrats. Plant species nomenclature follows Lambinon et al. (1998).

Data analysis

First, to explore overall differences in epi- and endozoochorous species composition, rank-abundance diagrams of the species dispersed by epizoochory and by endozoochory were designed. In addition, the log-transformed dataset of all zoochory samples together was used for Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980), using the program CANOCO 4.5 (ter Braak and Smilauer 2003). The sample-scores on the first four DCA-axes were then Spearman rank correlated (Siegel and Castellan 1988) with the date of sampling. The same ordination and correlation procedure was also used for the epizoochory and endozoochory samples separately.

Secondly, the species' abundance in the study area was Spearman rank correlated with the number of seedlings in the samples. This was done for the species in the combined "zoochorous" samples (n=66), the species exclusively in the epizoochory samples (n=13), the species exclusively in the endozoochory samples (n=37), and the species in both epi- and endozoochory samples (n=16), respectively.

Thirdly, morphological and ecological plant traits relevant for dispersal (Table 2, Appendix 1), were compared between a) species exclusively in epizoochory samples, b) species exclusively in endozoochory samples, c) species in both epi- and endozoochory samples, d) species in study area but not in zoochory samples. For this purpose, Kruskal Wallis tests and multiple comparisons (Siegel and Castellan 1988) were used for the continuous and ordinal variables, and Pearson χ^2 association tests (Siegel and Castellan 1988) for the categorical variables. All traits but plant height, strategy of dispersal and seedbank persistence (derived from Grime et al. 1988) originated from the BIOLFLOR database (Klotz et al. 2002), an elaborate database on biological and ecological traits of vascular plants in Germany.

Fourthly, all species in the study area were grouped into dispersal-functional plant types. These plant types were derived from cluster analysis, based on dispersal-relevant plant traits (Table 3), using Gower's Similarity Coefficient and the Sum of Squares method in the program Clustan Graphics 5.08 (Anon. 2001). The emergent clusters were tested for differences in these traits, using Kruskal Wallis tests with multiple comparisons for the continuous and ordinal variables, and

Pearson χ^2 association tests for the categorical ones. The clusters were subsequently named by a dispersal-functional plant type, on the basis of their cluster profiles. Finally, the number of species identified in the samples of a) exclusively epizoochory, b) exclusively endozoochory and c) both epi- and endozoochory, was used to link the dispersal-functional plant types with epi- or endozoochorous dispersal. To check whether the species abundance in the study area, which might influence the probability of zoochorous dispersal, differed between the different clusters, a Kruskal Wallis test with multiple comparisons was used. All statistical analyses were performed using the program SPSS 10 (Anon. 1999), unless mentioned otherwise.

Results

Species composition

From all samples together, 6675 seedlings of 66 plant species germinated, covering 20% of all species in the study area (Appendix 1, 2). The endozoochory samples contained more species and seedlings, and had a higher diversity than the epizoochory samples (Fig. 1). The most abundantly germinating species were *Urtica dioica* (70% of the seedlings in the endozoochory samples), *Cynoglossum officinale* and *Galium aparine* (41 and 31% of the seedlings in the epizoochory samples, respectively). The epizoochory samples contained relatively more grasses than the endozoochory samples (Appendix 1). Of the 66 species, 16 occurred in both epi- and endozoochory samples, 13 were exclusively present in the epizoochory samples and 37 only in the endozoochory samples.

The dissimilarity in species composition between the epi- and endozoochory samples was clearly reflected in

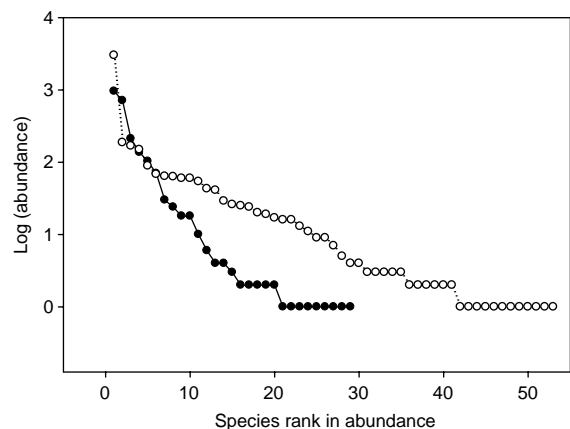


Fig. 1. Rank-abundance diagrams of dispersed plant species by epizoochory (filled symbols) and endozoochory (empty symbols). Species in each group are ranked from commonest (left) to rarest (right).

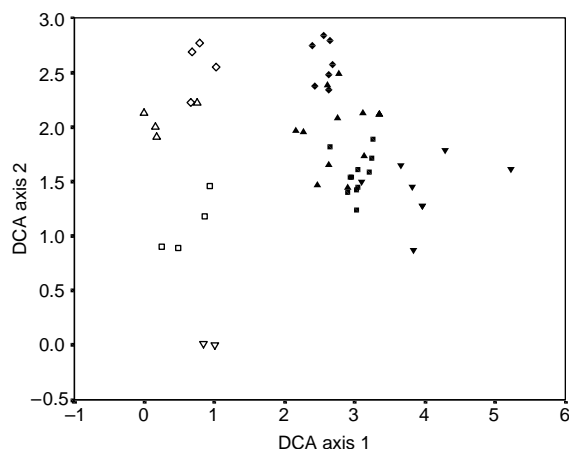


Fig. 2. First two axes of Detrended Correspondence Analysis (DCA) of all zoochory samples (filled symbols, epizoochory samples; empty symbols, endozoochory samples; downward pointing triangles, early summer; squares, mid-summer; upward pointing triangles, late summer; diamonds, early autumn). The percentages of explained variance are shown in Table 2.

the separation of both sample-groups along the first axis of the DCA-plot of all zoochory samples (Fig. 2). The second DCA-axis correlated strongest with date of sampling, indicating a seasonal variation in the species composition of the samples (Table 1). Also when the epi- and endozoochory samples were ordinated separately, the strong positive correlation of both first axes with date of sampling (Table 1) showed that time was a major factor explaining the variance within the epi- or endozoochory samples. The variation in axis scores among simultaneously collected samples illustrated the differences in species composition among seed loads of individual donkeys (Fig. 2).

Abundance in the study area

Species dominant in the study area (e.g. *Calamagrostis epigejos*, *Arrhenatherum elatius*, *Rubus caesius*) as well as rare species (e.g. *Leontodon saxatilis*, *Myosotis arvensis*) were dispersed zoochorously. The overall seedling density in the zoochory samples was positively correlated with species abundance in the study area

($n=66$, $r_s=0.33$, $p=0.006$). This correlation held true if only the species present in both epi- and endozoochory samples were regarded ($n=16$, $r_s=0.51$, $p=0.045$), but not for the exclusively epizoochorous species ($n=13$, $r_s=0.49$, $p=0.092$) and the exclusively endozoochorous species ($n=39$, $r_s=0.27$, $p=0.101$).

Plant traits of zoochorous species and species in the study area

A number of plant traits differed between the species in the study area that were present in the zoochory samples and those that were not present in the samples (Table 2). The latter contained relatively more tall, woody perennials with larger and heavier seeds (more berries and ant- or wind-dispersed seeds) and a transient seedbank. The group of species exclusively in the epizoochory samples contained relatively more biennial species, with adaptations for adhesive seed dispersal. The species exclusively in the endozoochory samples were generally smaller, mostly herbs, with smaller and lighter seeds, and a more persistent seedbank. Finally, the species in both epi- and endozoochory samples, comprised relatively more grasses, often with “unspecialized” seeds or seeds with adaptations to adhesive dispersal. The most significant differences existed between the species exclusively in the study area on the one hand, and the species exclusively in the endozoochory samples on the other hand, but this was probably partly due to the small size of the other groups.

Dispersal-functional plant types associated with epi- and endozoochorous dispersal

Five dispersal-functional plant types were derived from cluster analysis of the 335 species in the study area on the basis of dispersal-relevant plant traits (Table 3, Appendix 2). Tall woody perennials (shrubs and trees) with large, heavy berries or wind-dispersed seeds and a transient seedbank were the main constituents of cluster 1. Cluster 2 predominantly consisted of biennial grasses and herbs with intermediately long seeds, adapted to

Table 1. Percentage of explained variance of the first four DCA axes and Spearman rank correlation coefficients (r_s) between sample scores and date of sampling, for (a) epi- and endozoochory samples together ($n=55$), (b) epizoochory samples ($n=41$) and (c) endozoochory samples ($n=14$).

DCA axis	zoochory		epizoochory		endozoochory	
	% of expl. var.	r_s	% of expl. var.	r_s	% of expl. var.	r_s
1	14.6	-0.55***	18.3	0.94***	20.4	0.77**
2	6.1	0.81***	7.4	0.05 ns	9.7	0.51 ns
3	3.5	0.45**	3.8	-0.08 ns	5.7	0.25 ns
4	2.8	0.23 ns	1.8	0.29 ns	1.9	0.46 ns

*** $p < =0.001$; ** $p < =0.01$; ns, not significant.

Table 2. Overview of the traits associated with the following groups: (a) species in study area but not in zoochory samples; (b) species exclusively in epizoochory samples; (c) species exclusively in endozoochory samples; (d) species both in epi- and endozoochory samples.

		(a) exclusively study area	(b) exclusively epizoochory	(c) exclusively endozoochory	(d) epi+endo
number of species		269	13	37	16
seed weight (mg)	^k 18.6**	30.7 b	3.9 ab	1.1 a	0.9 ab
seed length (mm)	^k 16.2**	3.1 b	3.5 ab	1.7 a	2.0 ab
seed width (mm)	^k 22.4***	1.8 b	1.6 ab	0.9 a	0.8 a
plant height (ordinal 1–8)	8.5*	3.4 b	3.1 ab	2.4 a	3.2 ab
life span (ordinal 1–4)	^k 9.0*	3.3 b	2.3 a	3.0 ab	3.3 ab
dispersal strategy (categorical 1–6)	^c 47.3*** (15)	–12/7/–1/2/4/–1	7/–2/–1/–1/–1/–3	2/–3/3/–1/–2/1	2/–2/–1/0/–1/2
reproduction type (categorical 1–4)	^c 13.4 ns (12)	0/–4/1/3	0/6/–5/–1	0/–1/3/–1	0/0/1/–1
group (categorical 1–4)	^c 35.2*** (9)	–8/0/–5/13	2/–1/1/–3	0/1/5/–7	5/–1/–1/–3
seedbank persistence (ordinal 1–3)	^k 11.9**	2.2 a	2.2 ab	2.6 b	2.7 ab

Plant height (1, <100 mm; 2, 101–299 mm; 3, 300–599 mm; 4, 600–999 mm; 5, 1–3 m; 6, 3.1–6 m; 7, 6.1–15 m; 8, >15 m); life span (1, annual; 2, biennial; 3, annual/biennial to perennial; 4, perennial); dispersal strategy (1, adaptations for epizoochory; 2, ingested berries; 3, adaptations for anemochory; 4, adaptations for hydrochory; 5, adaptations for myrmecochory; 6, unspecialized); reproduction type (1, only by seed; 2, mostly by seed; 3, by seed and vegetative; 4, mainly or exclusively vegetative); group (1, grass; 2, sedge; 3, herb; 4, woody plant); seedbank persistence (1, transient; 2, short term persistent; 3, persistent).

^k Kruskal Wallis test (values are group averages and groups that differ significantly are indicated by different letters); ^c Pearson χ^2 association test (values are the differences between the observed and the expected values for the different categories. A positive value indicates an overrepresentation of the category in the cluster). *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns, not significant. Values between brackets are degrees of freedom.

epizoochory. Cluster 3 mainly grouped biennial herbs with light seeds, often with seed adaptations for dispersal by wind or ants, and cluster 4 contained predominantly perennial herbs with short seeds and various dispersal strategies. Biennial or perennial grasses, sedges and herbs with unspecialized seeds, often also reproducing vegetatively, were the main constituents of cluster 5. There was no significant difference in mean abundance in the study area between the member species of the different clusters. The species identified exclusively in the epizoochory samples nearly all belonged to cluster 2, while the species identified in both epi- and endozoochory samples had a broader distribution range. This range was even broader for the species occurring exclusively in the endozoochory samples (Table 3).

Discussion

Zoochory in a coastal dune ecosystem

As demonstrated in this study, epi- and endozoochory are important dispersal mechanisms in coastal dune ecosystems grazed by large herbivores. At least one fifth of all species (66 of 335 species) in the study area were dispersed by the donkeys (Appendix 1). Probably even more species would have been revealed if more samples over a larger time span had been collected. In addition, the seedling emergence method may underestimate both species and seed numbers (Couvreur et al. 2004c). On

the other hand, natural establishment rates of dispersed seeds may be considerably lower due to competition, predation and other environmental constraints (Edwards et al. 2000, Cosyns 2004).

The species composition of the epi- and endozoochory samples partially overlapped, but was clearly distinguishable in an ordination diagram (Appendix 1, Fig. 2). There was also a constant turnover in species composition of the zoochory samples in the course of the vegetation season (Table 1) (see also Malo and Suárez 1995b, Couvreur et al. 2004c), and the abundance of the species in the samples was correlated with the abundance in the study area, at least for those species occurring in both epi- and endozoochory samples.

Trees and shrubs seemed, with the exception of *Rubus caesius*, not to be dispersed zoochorously (Tables 2 and 3, see also Fischer et al. 1995, Stender et al. 1997, Heinken et al. 2002). Besides possibly unsuitable germination conditions, the relatively small amount of species with fleshy berries (e.g. *Rubus caesius*, *Solanum nigrum*) germinating from the donkey dung, may also suggest that these species are better adapted for dispersal by frugivorous birds than by large herbivores. Further investigation may elucidate this. A number of other plant traits differed between the species in the study area which were present in the zoochory samples, and those which were not (Table 2), and between the different clusters associated with the different types of zoochory (Table 3). Morphological seed properties such as seed size and seed weight seemed important indicators for

Table 3. Overview of the traits used to define dispersal-functional plant type clusters (named by their predominant profile). In addition, the abundance of the species in the study area is given, as well as the number of species identified in the exclusively epizoochory samples, the exclusively endozoochory samples, or in both. Finally, the last three rows show percentage of all cluster species in the former groups.

cluster number dispersal-functional type		1 Tall woody perennials with large, heavy seeds (berries or wind-dispersed) and a transient seedbank	2 Biennial grasses and herbs with intermediately long seeds adapted to epizoochory	3 Biennial herbs with light seeds adapted to dispersal by wind and ants	4 Perennial herbs with short seeds and various dispersal strategies	5 Biennial or perennial grasses, sedges and herbs with unspecialized seeds, often also reproducing vegetatively
number of species in cluster	total = 335	74	63	51	77	70
seed weight (mg)	^k 58.6***	98.07 b	2.93 a	1.39 a	13.64 a	2.90 a
seed length (mm)	^k 62.0***	4.93 c	3.13 b	2.34 ab	1.90 a	2.33 ab
seed width (mm)	^k 66.3***	3.29 b	1.29 a	1.13 a	1.14 a	1.25 a
plant height (ordinal 1–8)	^k 144.7***	5.72 b	2.51 a	2.51 a	2.53 a	2.53 a
life span (ordinal 1–4)	^k 114.8***	4.00 c	2.61 ab	2.19 a	3.92 c	2.97 b
seedbank persistence	^k 35.4***	1.38 a	2.19 b	2.55 b	2.47 b	2.40 b
dispersal strategy (categorical 1–6)	^c 540.8*** (20)	–11/29/6/–1/–6/–17	36/–7/–14/–3/–4/–8	–10/–7/24/1/10/–18	–4/–5/4/4/2/–1	–11/–10/–19/–1/–3/44
reproduction type group (categorical 1–4)	^c 236.2*** (16)	1/–2/1/0	19/–16/–2/0	27/–23/–4/0	–44/47/–5/2	–2/–7/10/0
abundance in the study area	^c 374.8*** (12)	–6/–1/–46/54	14/0/–4/–11	–6/–3/22/–13	–9/2/23/–16	7/3/5/–14
sp. excl. in epi	^k 7.0 ns	1.86 a	2.14 a	2.06 a	1.84 a	2.06 a
sp. excl. in endo		0	10	3	0	0
sp. excl. in epi+endo		2	6	9	12	8
% cluster sp. excl. in epi		0	5	3	2	6
% cluster sp. excl. in endo		0	16	6	0	0
% of sp. in epi+endo		3	10	18	16	11
		0	8	6	3	9

Plant height (1, <100 mm; 2, 101–299 mm; 3, 300–599 mm; 4, 600–999 mm; 5, 1–3 m; 6, 3.1–6 m; 7, 6.1–15 m; 8, >15 m); life span (1, annual; 2, biennial; 3, annual/biennial to perennial; 4, perennial); seedbank persistence (1, transient; 2, short term persistent; 3, persistent); dispersal strategy (1, adaptations for epizoochory; 2, ingested berries; 3, adaptations for anemochory; 4, adaptations for hydrochory; 5, adaptations for myrmecochory; 6, unspecialized); reproduction type (1, only by seed; 2, mostly by seed; 3, by seed and vegetative; 4, mainly or exclusively vegetative); group (1, grass; 2, sedge; 3, herb; 4, woody plant); abundance in the study area (1, present; 2, occasional; 3, frequent; 4, codominant; 5, dominant). ^k Kruskal Wallis test (values are cluster averages and clusters that differ significantly are indicated by different letters); ^c Pearson χ^2 association test (values are the differences between the observed and the expected values for the different categories. A positive value indicates an overrepresentation of the category in the cluster). *** $p < = 0.001$; ns, not significant. Values between brackets are degrees of freedom.

zoochorous dispersal, as well as special dispersal adaptations. The latter seemed more indicative in the case of epizoochory than in the case of endozoochory. Still, a much wider range of dispersal adaptations was represented among the epi- and endozoochorously dispersed species than previously assumed (see Grime et al. 1988, Appendix). For endozoochory, small and light seeds, a small plant size and a persistent seedbank (see also Pakeman et al. 2002) seemed important determinants, while adhesive seed adaptations and a short life span seemed associated with epizoochory. The species identified in both epi- and endozoochory samples often possessed intermediate traits.

Pakeman et al. (2002) suggested that many species adapted to endozoochory by large herbivores might be hidden in the dispersal strategy category "unspecialized" (Grime et al. 1988). These species lack obvious seed adaptations and use their edible vegetative parts as ecological "fruits" to attract herbivores as seed dispersers. Janzen (1984) formulated this "foliage is the fruit" hypothesis in the context of endozoochory. However, the presence of many grasses with unspecialized seeds in our epizoochory samples (Appendix 1 and 2, see also Couvreur et al. 2004c) may suggest that the "foliage is the fruit" hypothesis might not only apply to endozoochory, but also to epizoochory. Apparently, not only specialized seed adaptations increase the chance of dispersal in the fur of herbivores, but also increasing the chance that animals come into contact with the seeds, by providing a food source. The fact that the inflorescence of many grasses is physically separated from the edible leaves by a tall stem, may further enhance the probability of adherence of the seeds to the fur of grazing herbivores. Edibility might thus enhance both forms of zoochory.

Complementarity of epi- and endozoochory

The differences in species composition between the epi- and endozoochory samples, as well as the different association of dispersal-functional plant types with either of the mechanisms demonstrate the complementarity of epi- and endozoochory. This complementarity seemed to be more pronounced than the additive effect of epi- and endozoochory, since only 16 species were dispersed by both mechanisms and 50 species by only one of the mechanisms. In addition, the different association of epi- and endozoochory with the dispersal-functional plant types revealed an increasing degree of specificity from endozoochory towards epizoochory, since the endozoochorously dispersed species covered many more dispersal-functional plant types than those dispersed by epizoochory. Although endozoochory is supposed to have a greater impact than epizoochory on vegetation dynamics in terms of quantity of seed

dispersal (Janzen 1984), both mechanisms are ecologically important and complementary. The combination of epi- and endozoochory results not only in a larger number of dispersed seeds, but, more importantly, in a larger spectrum of dispersed species. This is a consequence of the different constraints of both mechanisms. Whereas e.g. grooming behaviour of animals can limit epizoochory (Sorensen 1986, Kiviniemi 1996), endozoochorous dispersal is constrained by seed survival in the digestive tract (Neto and Jones 1987, Gardener et al. 1993, Cosyns 2004) and by feeding preferences of herbivores. Yet, the general relative ecological significance of both dispersal modes as compared to each other but also compared to other possible long-distance seed dispersal modes needs further investigation.

Consequences for nature management

As large herbivores have always been part of natural ecosystems, their complementary role as epi- and endozoochorous dispersal vectors may be important for maintaining species richness. Grazing by livestock has recently become an important nature management tool for conservation and restoration of many habitats in northern temperate regions (see also Couvreur et al. 2004c). Until now, much attention was given to the contribution of livestock to plant diversity patterns, both at the local and landscape scale, through their activities of selective grazing, trampling and defecating, which influence processes that enhance local extinction rates. Yet herbivores may also influence plant diversity through processes that affect colonisation rates (Olf and Ritchie 1998). The results of this paper clearly show the importance of large herbivores as long-distance seed dispersal vectors for much more plant species than could be assumed from their morphological seed characteristics (see also Couvreur et al. 2004a, b, c). Retention times of seeds in the fur (see Couvreur et al. 2004b) and in the digestive tract of large herbivores (Cosyns 2004) allow dispersal over distances of metres to kilometers, hence covering the entire 100 ha study area. The growing evidence for the role of large herbivores in the seed dispersal process urges for a well-considered nature management policy which not only focuses on amelioration of habitat conditions, but also considers the spatial arrangement of suitable but still unoccupied patches for critical plant species. If plants can bridge gaps in space and time, this may favour a sustainable conservation of critical plant populations. It is shown here that the use of large herbivores like donkeys as managers, might help to reach this goal, through the epi- and endozoochorous dispersal of plant seeds.

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Appendix 1. Overview of the species in the zoochory samples and their relevant traits.

Species	presence in epi/endo	plants in epi samples	plants in endo samples	number of epi samples	number of endo samples	abundance in study area	seed weight (mg)	seed length (mm)	seed width (mm)	plant height	life span	dispersal strategy	reproduction type	group	seedbank persistence	cluster number dispersal – functional plant type
<i>Achillea millefolium</i>	2	0	4	0	3	3	0.13	2	0.86	2	4	3	2	3	1	4
<i>Agrostis capillaris</i>	12	3	29	2	8	2	0.06	1.00	0.38	2	4	6	2	1	3	5
<i>Agrostis stolonifera</i>	2	0	41	0	5	2	0.08	1.08	0.45	2	4	6	2	1	3	5
<i>Aira praecox</i>	2	0	3	0	2	2	0.18	2.52	0.48	1	1	1	1	1	2	2
<i>Anthriscus caucalis</i>	12	211	1	14	1	4	1.3	3.77	0.96	3	1	1	1	3	.	2
<i>Arctium minus</i>	1	137	0	6	0	2	7.38	5.73	2.24	5	2	1	1	3	3	2
<i>Arenaria serpyllifolia</i>	2	0	13	0	6	4	0.05	0.6	0.44	1	1	3	1	1	3	3
<i>Arrhenatherum elatius</i>	1	30	0	9	0	5	3.29	3.81	1.22	5	4	1	1	1	1	2
<i>Artemisia vulgaris</i>	12	1	68	1	4	2	0.13	1.46	0.44	5	4	6	1	3	3	5
<i>Bidens tripartita</i>	1	1	0	1	0	1	2.61	6.36	2.18	3	1	1	1	3	.	2
<i>Bromus hordeaceus</i>	1	2	0	1	0	3	3.48	6.08	1.51	3	1	1	1	1	1	2
<i>Calamagrostis epigejos</i>	2	0	26	0	5	5	0.10	1.25	0.4	4	4	3	2	1	.	1
<i>Capsella bursa-pastoris</i>	2	0	1	0	1	3	0.13	0.95	0.47	1	1	3	1	3	3	3
<i>Carex arenaria</i>	2	0	187	0	14	4	0.78	1.83	1.08	2	4	6	3	2	.	5
<i>Cerastium fontanum</i>	2	0	3	0	2	3	0.12	.	.	1	4	6	2	3	3	4
<i>Cerastium semidecandrum</i>	1	4	0	3	0	3	0.04	0.45	0.41	2	1	3	1	3	3	3
<i>Chelidonium majus</i>	2	0	2	0	2	3	0.83	1.36	0.81	3	4	5	1	3	3	3
<i>Chenopodium album</i>	2	0	1	0	1	2	1.5	1.17	1.17	5	1	6	1	3	3	5
<i>Conyza canadensis</i>	2	0	2	0	2	3	0.05	1.21	0.34	3	1	3	1	3	.	3
<i>Crepis capillaris</i>	2	0	2	0	2	4	0.26	2.20	0.53	2	1	3	1	3	3	3
<i>Cynoglossum officinale</i>	1	957	0	32	0	3	26.05	6.78	5.6	3	3	1	1	3	2	2
<i>Dactylis glomerata</i>	1	1	0	1	0	2	0.99	2.77	0.99	3	4	6	1	1	1	2
<i>Epilobium ciliatum</i>	12	1	1	1	1	1	0.07	1.13	0.4	4	4	3	2	3	2	4
<i>Epilobium hirsutum</i>	2	0	2	0	1	2	0.14	0.98	0.44	5	4	3	2	3	3	4
<i>Epilobium montanum</i>	2	0	1	0	1	2	0.12	1.18	0.48	3	4	3	2	3	3	4
<i>Eupatorium cannabinum</i>	2	0	4	0	3	3	0.27	2.97	0.52	5	4	3	2	3	3	4
<i>Festuca rubra</i>	12	4	2	2	2	3	1.30	3.83	1	2	4	6	2	1	1	5
<i>Galium aparine</i>	12	712	60	19	13	4	8.34	3.2	2.63	4	1	1	1	3	1	2
<i>Galium mollugo</i>	2	0	54	0	2	2	0.53	1.22	1.13	3	4	1	1	3	.	2
<i>Galium verum</i>	2	0	60	0	6	4	0.44	1.42	1.2	2	4	6	2	3	1	4
<i>Geranium molle</i>	2	0	5	0	2	3	1.24	1.54	1.09	2	1	6	1	3	2	5
<i>Geum urbanum</i>	1	1	0	1	0	2	2.45	4.54	1.75	3	4	1	1	3	2	2
<i>Holecus lanatus</i>	12	10	89	9	9	4	0.47	2.35	0.84	3	4	6	2	1	3	5
<i>Hypochaeris radicata</i>	2	0	2	0	1	2	.	6.00	0.75	1	4	3	1	3	2	3
<i>Juncus articulatus</i>	2	0	17	0	7	2	0.02	0.57	0.27	3	4	1	2	2	3	4
<i>Juncus bufonius</i>	2	0	16	0	7	2	0.02	0.39	0.31	1	1	1	1	2	3	2
<i>Koeleria albescens</i>	2	0	3	0	2	3	.	.	.	2	4	6	2	1	.	5
<i>Leontodon saxatilis</i>	2	0	1	0	1	1	.	.	.	2	4	3	2	3	2	4

Appendix (Continued.)

Species	presence in epi/endo	plants in epi samples	plants in endo samples	number of epi samples	number of endo samples	abundance in study area	seed weight (mg)	seed length (mm)	seed width (mm)	plant height	life span	dispersal strategy	reproduction type	group	seedbank persistence	cluster number dispersal – functional plant type
<i>Lythrum salicaria</i>	12	6	25	2	4	2	0.05	1.03	0.4	4	4	4	1	3	3	3
<i>Myosotis arvensis</i>	1	24	0	11	0	1	0.29	1.43	0.89	2	2	1	1	3	3	2
<i>Oenothera biennis</i>	1	70	0	6	0	3	0.44	1.7	1.25	4	2	3	1	3	.	3
<i>Oenothera glazioviana</i>	2	0	19	0	3	3	0.6	1.51	1.24	4	2	3	1	3	.	3
<i>Phleum arenarium</i>	1	2	0	2	0	3	0.18	1.03	0.6	1	1	1	1	1	.	2
<i>Phleum pratense</i>	12	2	63	2	13	1	1.00	1.48	0.91	3	4	1	1	1	3	2
<i>Plantago coronopus</i>	2	0	1	0	1	2	.	1.1	0.65	1	3	1	1	3	3	2
<i>Plantago lanceolata</i>	2	0	16	0	4	2	1.81	2.84	1.39	2	4	1	1	3	3	2
<i>Plantago major</i>	12	1	43	1	3	3	0.26	1.5	0.81	2	4	1	1	3	3	2
<i>Poa annua</i>	12	2	24	2	7	3	0.30	1.86	0.7	2	3	6	1	1	3	2
<i>Poa pratensis</i>	12	1	149	1	14	3	0.30	1.60	0.52	3	4	6	2	1	3	5
<i>Poa trivialis</i>	12	18	168	11	12	4	0.17	1.52	0.5	3	4	6	2	1	3	5
<i>Ranunculus repens</i>	2	0	1	0	1	2	1.82	3.09	2.27	2	4	4	2	3	3	4
<i>Rubus caesius</i>	2	0	3	0	3	5	3.61	3.13	1.93	4	4	2	2	4	2	1
<i>Rumex crispus</i>	2	0	1	0	1	2	2.93	2.51	1.58	3	4	6	2	3	3	4
<i>Rumex obtusifolius</i>	1	1	0	1	0	2	2.70	2.29	1.4	3	4	1	1	3	3	2
<i>Sagina procumbens</i>	2	0	1	0	1	3	0.02	0.43	0.27	1	4	6	1	3	3	5
<i>Senecio jacobaea</i>	12	18	9	7	5	4	0.39	2.02	0.5	4	3	3	1	3	3	3
<i>Silene latifolia</i> subsp. <i>alba</i>	2	0	3	0	2	3	0.81	1.35	1.1	4	4	3	1	3	3	3
<i>Solanum nigrum</i>	2	0	1	0	1	2	0.74	1.92	1.36	2	1	2	1	3	.	3
<i>Sonchus asper</i>	1	1	0	1	0	2	0.34	2.70	1.06	3	1	3	1	3	3	3
<i>Sonchus oleraceus</i>	12	2	9	2	6	2	0.53	2.86	0.91	3	1	3	1	3	3	3
<i>Stellaria media</i>	2	0	7	0	5	4	0.48	1.13	1.05	2	1	6	1	3	3	5
<i>Trifolium dubium</i>	2	0	11	0	3	3	0.36	1.25	0.86	2	1	1	1	3	3	2
<i>Trifolium repens</i>	2	0	20	0	3	2	0.59	1.17	1.02	1	4	1	2	3	3	4
<i>Urtica dioica</i>	12	103	3010	17	10	3	0.19	1.19	0.77	4	4	1	2	3	3	4
<i>Veronica chamaedrys</i>	2	0	64	0	10	3	0.22	1.18	1	1	4	6	2	3	3	4
<i>Vicia cracca</i>	2	0	1	0	1	4	14.29	2.89	2.81	4	4	6	1	3	1	5

Presence in epi/endo samples (1, epizoochory samples; 2, endozoochory samples; 12, both epi- and endozoochory samples); abundance in the study area (1, present; 2, occasional; 3, frequent; 4, codominant; 5, dominant); plant height (1, <100 mm; 2, 101–299 mm; 3, 300–599 mm; 4, 600–999 mm; 5, 1–3 m; 6, 3.1–6 m; 7, 6.1–15 m; 8, >15 m); life span (1, annual; 2, biennial; 3, annual/biennial to perennial; 4, perennial); dispersal strategy (1, adaptations for epizoochory; 2, ingested berries; 3, adaptations for anemochory; 4, adaptations for hydrochory; 5, adaptations for myrmecochory; 6, unspecialized); reproduction type (1, only by seed; 2, mostly by seed; 3, by seed and vegetative; 4, mainly or exclusively vegetative); group (1, grass; 2, sedge; 3, herb; 4, woody plant); seedbank persistence (1, transient; 2, short term persistent; 3, persistent); cluster number (see legend of Appendix 2).

Appendix 2. All plant species in the study area, clustered in dispersal-relevant functional plant types. The species are represented by the first four letters of genus resp. species name (first four letters in capitals, species identified exclusively in epizoochory samples; last four letters in capitals, species identified exclusively in endozoochory samples; all letters in capitals, species identified both in epi- and endozoochory samples).

Cluster 1		Cluster 2		Cluster 3		Cluster 4		Cluster 5	
acerpseu	rosarugo	agrieupa	trifcamp	ancharve	ConyCANA	AchiMILL	mentaqua	aegopoda	stelpall
popucand	sympalbu	CYNOoffi	TrifDUBI	fumaoffi	sisyoffi	vincmajo	apiurepe	allivine	gerapusi
tiliplat	cotohori	GEUMurba	BIDEtrip	lamipurp	senevisc	epillanc	ranuflam	fallaube	veropers
fraxexce	RubuCAES	ranuacri	GALIAPAR	mercannu	senevulg	sedurupe	RanuREPE	cardprat	vicilath
carpbetu	rubufruc	helinum	ARCTminu	verohede	SONCasp	ceratome	carepani	convarve	anagarve
ulmino	cotosimo	ballnigr	arctpube	clayperf	SONCOLER	LeonSAXA	hydrvulg	lemnmino	StelMEDI
betuspp	ribeuvac	RUMEobtu	MYOSarve	lamiamp	lacterr	orobcary	lysvulg	potacris	matrmatr
pinunigr	hedeheli	GaliMOLL	torijapo	lamihybr	senesyv	pyrorotu	dantdecu	ranutric	vichirs
popualba	rosapimp	PlanLANC	erodlebe	anchoffi	carlvulg	hierpilo	luzucamp	orniumbe	fallconv
popubals	mahoaqui	PLANMAJO	myosramo	CheMAJU	cirspalu	seduacre	JuncARTI	ranufica	polypers
popucans	prunspin	ranubulb	myosstric	theshumi	pastati	veroanag	juncsubn	AGROCAPI	fumamura
saliaiba	cratmono	thympule	PlanCORO	polyserp	SENEJACO	epilangu	scirseta	KoelALBE	ChenALBU
pinusylv	prunsero	juncinfl		polyvulg	cirsvulg	hierumbe	bellpere	AgroSTOL	chenrubr
clemvita	pyrucomm	PHLEPRAT		violcani	crepbien	pulidyse	poteanse	HOLCLANA	vicisati
salimult	prunaviu	anthodo		violcurt	OENObien	EPILCILI	nastoffi	miliieffu	anthsyv
salicapr	pruncera	avenpube		bryodioi	OenoGLAZ	seneeruc	RumeCRIS	POAPRAT	chaetemu
ammoaren	euoneuro	ARRHelat		SolaNIGR	verbthap	cirsarve	thalminu	POATRIV	centthui
phraust	rosacaes	triseflav		erigacer	diptenu	sapooffi	potereec	elumobtu	rumeprat
CalaEPiG	franalnu	holmoll		tragprat	taraspp	EpiHIRS	poterept	elymath	lathprat
humulupu	rosacani	DACTglom		heraspho	silenuta	EupaCANN	cardhirs	glycnota	ViccCRAC
salirepe	vibulant	festarun		LYTHSALI	HypoRADI	EpilMONT	ceraarve	glycflui	lithoffi
syrivulg	malusylv	festgiga		rumecong	siledioi	hypeperf	CeraFONT	poapalu	aquivulg
poputrem	sorbauc	festfili		myoscaesp	silevulg	lychflos	rumeacet	festjunci	centjace
salifrag	liguvulg	lolipere		ranuscel	SileLATI	epiphell	VeroCHAM	FESTRUBR	centnigr
saliatro	rosatome	molicaer		rumemari		hypetetr	verooffi	CareAREN	ARTEVULG
salicine	rosaobtu	POAANNU		arabthal		inucony	potester	careflacc	aspecyna
alnuglut	rosarubi	AiraPRAE		gnaplute		arumital	saginodo	elymrepe	SagiPROC
alnuinca	ribealpi	bromthom		CapsBURS		aspaoffi	galaniva	leymaren	lotucorn
cladmari	ribenigr	PHLEaren		centeryt		sambebul	lamigale	caredist	arabhirs
eleopalu	ribeodor	JuncBUFO		saxitrid		soladulc	lamialbu	carehirt	jasimont
coluarbo	riberubr	aperinte		centpulc		groendens	lamimacu	caretrin	moehtrin
labuanag	ribesang	BROMhord		CERAsemi		calysepi	glechede	careviri	
ononrepe	sambnigr	hordmuri		sileconi		hemespp	violhirt	allipeti	
rhushirt	prundome	bromtect		CrepCAPI		galiulig	myosscor	chenmura	
robipseu	querrobu	bromster		centlitt		rheum	prunvulg	GeraMOLL	
cornsang		ANTHCAUC		diplmura		GaliVERU	TrifREPE	gerarober	
lycibarb		urtiuren		eropvern		thalflav	zannpalu	ceradiff	
rubuidae		erodcicu		ArenSERP		apiunodi	URTIDIOI	veroarve	
hipprham		myosdisc		corycane		galipalu		cochdani	

Cluster legend: 1, predominantly tall woody perennials with large, heavy seeds (berries or wind-dispersed); 2, predominantly biennial grasses and herbs with intermediately long seeds, adapted to epizoochory; 3, predominantly biennial herbs with light seeds, adapted for dispersal by wind and ants; 4, predominantly perennial herbs with short seeds and various dispersal strategies; 5, predominantly biennial or perennial grasses, sedges and herbs with unspecialized seeds, reproducing by seed or vegetatively.