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Large herbivores in coastal dune management: do grazers do what they are supposed to do?

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Abstract

After some decades of rather sparse and more or less ad-hoc nature management (*e.g.* local shrub-cutting, sod-cutting, mowing), the manager of the Flemish coastal nature reserves [Nature Department (Coastal Zone Management Cell) of AMINAL, Ministry of the Flemish Community] decided to introduce a more coherent and relatively large-scale nature management approach. Since the mid-nineties, several large areas were cleared from scrubs and in the larger nature reserves different herbivore species were introduced. On historical grounds and based on general management expectations, several ungulate species were introduced (sheep, donkeys and different horse and cattle breeds). Since the herbivore introductions from 1997 onwards, research has been done on the foraging behaviour and habitat use, diet selection and preference of some of the introduced herbivores and on their potential contribution to seed dispersal. Above that, several monitoring research programmes were carried out, following the impact of the ungulates on flora, vegetation and different faunal groups in order to evaluate the effectiveness of grazing in realizing the predefined management goals. Here we summarize some results of the research focussing on the driving forces in grazing management and try to conclude on the impact they will have through their habitat use, foraging behaviour, diet selection and other behavioural aspects. We formulate generalized conclusions on the suitability and usefulness of year round grazing by domestic animals in these rather low productive, spatially and temporally heterogeneous dune ecosystems.

Keywords: Nature management; Grazing; Seed dispersal; Coastal dune; Monitoring.

Introduction

After a general ecosystem vision for the Flemish coast was realized (Provoost and Hoffmann, 1996), and management plans for the larger Flemish coastal Nature Reserves (Houtsaegerduinen and Westhoek) were made (Hoys *et al.*, 1996ab), the manager of both nature reserves decided to start with grazing as main management measure in at least part of both reserves. Before grazers were introduced in the latter nature reserve, large parts, dominated by scrubs of Sea-buckthorn (*Hippophae rhamnoides*) and Wild privet (*Ligustrum vulgare*) were cut down and removed first. Before 1996, local

management measures had been undertaken at several locations, but never at a large scale (sod-cutting, mowing, local shrub cutting and juvenile shrub uprooting, …).
Grazing management has been implemented to maintain species-rich, alkaline dune grassland (so-called *Polygalo-Koelerion* within the *Cladonio-Koelerietalia*) (Provoost *et al.*, 2004) and to avoid further growth of the dense scrubs that cover large parts of both areas. Conservation management concentrates on the prevention of further expansion of dominant, highly competitive graminoids, like *Calamagrostis epigejos, Holcus lanatus* or *Arrhenatherum elatius* and shrub species, such as *Hippophae rhamnoides* and *Ligustrum vulgare*. It was expected that the herbivores would decrease the vitality and abundance of at least some of these competitive species through direct consumption or through damage induced by trampling and movement patterns. Likewise, grazing was expected to create structural diversity within monotonous vegetations, due to the dominance of one of the aforementioned plant species. Finally, conservation management also hoped that fragile habitats that are rather vulnerable to intensive grazing activity, like alkaline moss-dominated grey dunes (so-called *Tortulo-Koelerion* within the *Cladonio-Koelerietalia*), would not lose their dune specific species diversity due to trampling activity.
Since the introduction of large grazers from 1997 onwards, monitoring takes place, using an ex-/enclosure technique (described by Bonte *et al.*, 1998; Provoost *et al.*, 2004). Response variables that are monitored are flora, vegetation, terrestrial arthropods (mainly focussing on spiders, ground and dung beetles) and avifauna.
Parallel to this monitoring initiative, more fundamental research is being done on habitat and diet selection (Lamoot, 2004) and on seed dispersal through ungulate endozoochory (Cosyns, 2004) and epizoochory (Couvreur, 2005; Couvreur *et al.*, 2005b). Since the monitoring programme started in 1996, a large quantity of publications, reports and MSc-theses were published (an up-to-date list is given in Anonymus, 2005). Not all of these publications deal with nature management in a direct sense, reason why they are not found, when screening international literature on its relevance for nature management (Bonte and Hoffmann, 2005).
Here, we will primarily focus on the introduced domestic herbivores, on their habitat use and foraging behaviour, their diet selection and their possible contribution to endozoochorous plant seed dispersal. We will refer to some of the monitoring results to underpin conclusions on the realization of management goals.

Methods

General research methodology on the driving forces, *i.e.* the introduced herbivores, is described thoroughly in Lamoot *et al.* (2004b, 2005) and Cosyns (2004) for the study of habitat use, foraging behaviour and diet selection of large herbivores and in Cosyns and Hoffmann (2005) and Cosyns *et al.* (2005) for research of endozoochorous seed dispersal. Here, we include data collected from donkeys grazing in the FNR the Houtsaegerduinen since 1997, from Shetland pony and Scottish Highland cattle grazing in the FNR Westhoek (southern grazing block) since 1997 and 1998, respectively, from Konik pony and Scottish Highland cattle grazing in the FNR Westhoek (northern grazing block) since 1998, from Shetland pony grazing in the Doornpanne since 1996, from Mergelland sheep and rabbit in the FNR Ter Yde and IJzermonding (sheep since 1999),

from Haflinger pony and rabbit in the Fossile dunes of Ghyvelde (France) (ponies since 1996) and from Galloway cattle in the FNR D'Heye since 1998.

Results

Habitat use, forage behaviour and diet of large herbivores

Since most herbivores were grazing in different areas, each with their specific dune habitats and their area-specific spatial arrangement, we cannot compare habitat use and forage behaviour of those herbivores in an absolute sense. To be able to give a relatively reliable comparison we therefore lumped the initially distinguished vegetation types into a restricted number of structurally defined vegetation groups. Even then, comparison is not always possible, since those structurally defined habitats do not necessarily show the same floristic composition and spatial arrangement. Nonetheless, we believe general conclusions can be drawn from the observations on the use of grassy habitat, scrub and woodland (Table I). Cattle, horse breeds and donkeys show quite different grazing investment. While the only ruminant spends only 38% of its time on foraging (excluding rumination time), donkeys spend more than half of their time on foraging, while both horse breeds need up to ¾ of their time to collect their food. All grazer species show strong preference for grassy habitat and for graminoid forage. None of the species shows much interest in scrubs or woody plants, but interspecific differences do occur. Cattle are more often grazing in woody environment than the horse breeds; donkeys take an intermediate position. None of the animals focuses on woody plants as food object though. Within scrub and woodland, all species remain to their preference for graminoid food. As far as number of bites is concerned, forbs are hardly different from woody species, being far less favoured than graminoids by all herbivore species (Table I).

Looking at a higher resolution lever for habitat preference indications (Table II) as far as grazing is concerned, in which relative area taken by every vegetation type per site is taken into account, we find that grasslands, if available, are highly preferred, followed by rough grassland if grassland is not at hand. We should keep in mind though, that spatial arrangement of vegetation types is not taken into consideration. Donkeys are avoiding scrub strongly, while all grassy habitats are preferred or strongly preferred. The only herbivore species showing some preference for woodland is cattle.

Mean grazing time and mean daily grazing time per ha of a particular vegetation type give a good general idea of the consumption within these vegetation types, and, hence, of the potential impact of grazing on these vegetation types (Table III). Keeping in mind that spatial arrangements of vegetation types are different between sites, we notice that donkeys spent more time in sparsely vegetated dune habitats, than cattle and Shetland pony, although not consistently through time. Again, data are strongly influenced by the fact that cattle spent far less time on foraging than the horse breeds and donkeys. Although cattle show grazing preference for grassland and grassland with shrub invasion, they spent less time there than the Shetland ponies, their companions at the same site.

Table I. Mean values of several grazing variables based on continuous focal animal sampling during six hour sessions (Lamoot *et al.*, 2004b), averaged over one year for Scottish Highland Cattle (C), Shetland pony (S) and Haflinger pony (H) and over three years for Donkeys (D). Distinguished general vegetation groups are grassy vegetation, scrub and woodland. Distinguished forage classes are graminoids (all monocots), forbs (non-woody dicots) and woody plants. GT(%): percentage of total time spent on grazing; Bite rate: # bites per minute grazing; n.a.: data not available. Mean body weights: Scottish Highland cows: 481±21kg; Highland bulls: 520±43kg; Shetland mares: 205±8kg, donkey mares:175±7kg (Haflinger mare body weight not measured). Highland cattle and Shetland ponies graze in the Flemish Nature Reserve the Westhoek (data from the southern grazing block of approx. 60ha), donkeys graze in the FNR Houtsaegerduinen (approx. 79ha), Haflinger ponies graze in the NW-French fossile dunes of Ghyvelde (approx. 60ha). Adapted from Lamoot (2004)

Dependent variable	**Independent variable**	**C**	**S**	**D**	**H**
General grazing variables					
GT (%)		38	71	56	68
# bites.h^{-1}		703	1339	444	n.a.
Bite rate		29.2	31.5	14.3	n.a.
GT (%).habitat^{-1}					
	Grassy	59	77	70	95
	Scrub	24	13	23	3
	Woodland	17	10	10	2
% of bites. habitat^{-1}					
	Grassy	75	81	74	n.a.
	Scrub	14	9	17	n.a.
	Woodland	11	10	9	n.a.
% of bites.forage class^{-1}					
	Graminoids	87	91	80	n.a.
	Forbs	8	9	11	n.a.
	Woody	5	0	9	n.a.
% of bites.habitat^{-1}.forage class^{-1}					
	Grassy				
	Graminoids	65	74	59	n.a.
	Forbs	6	7	8	n.a.
	Woody	4	0	7	n.a.
	Scrub				
	Graminoids	12	8	14	n.a.
	Forbs	1	1	2	n.a.
	Woody	1	0	1	n.a.
	Woodland				
	Graminoids	10	9	7	n.a.
	Forbs	1	1	1	n.a.
	Woody	0	0	1	n.a.

Table II. Jacobs' index of selection (Jacobs, 1974) of Highland cattle (C), Shetland ponies (S), Donkeys (D) and Haflinger ponies (H) for different vegetation types: $D_i = (p_i - A_i)/((p_i + A_i) – (2* p_i*A_i))$ with p_i the mean proportion of the total grazing time spent in the *i*th vegetation type and A_i the proportion of the area covered by the *i*th vegetation type. The value of D_i ranges from -1 to +1, with negative and positive values indicating avoidance and selection of the vegetation type, respectively: strong avoidance (--): $D_i < -0.4$; avoidance (-): $-0.4 < D_i < -0.08$; no selection (0): $-0.08 < D_i < 0.08$; preference (+): $0.08 < D_i < 0.4$; strong preference (++): $D_i > 0.4$. Adapted from Lamoot (2004)

Vegetation type	Westhoek			Houtsaegerduinen		Ghyvelde	
	Area (%)	C	S	Area (%)	D	Area (%)	H
Grasslands	9	++	++	5	++	0	
Moss dunes & open vegetation	11	--	-	8	++	35	-
Rough grasslands (*)	8	-	++	4	++	32	++
Grassland with shrub invasion	7	+	+	2	+	0	
Rough vegetation	9	0	0	4	++	3	--
Scrub	41	-	--	67	--	7	--
Woodland	14	+	-	11	0	23	--

(*) Rough grassland is dominated by *Carex arenaria* in Ghyvelde, in both other areas the dominant graminoid is *Calamagrostis epigejos*.

Table III. Mean grazing time per hour, registered during six-hour sessions (in $min.h^{-1}$) and mean daily grazing time per ha ($min.ha^{-1}$) of a particular vegetation type for Scottish Highland cattle (C) , Shetland ponies (P), both grazing in Westhoek-South (data of 2001) and Donkeys (D), grazing in Houtsaegerduinen (data of 1998 and 2000). GT: grazing time in minutes per hour, not including ruminating (cattle). Adapted from Lamoot (2004)

Vegetation type	Westhoek-South				Houtsaegerduinen			
	2001				1998		2000	
	C	C	S	S	D	D	D	D
	$min.h^{-1}$	$min.ha^{-1}$	$min.h^{-1}$	$min.ha^{-1}$	$min.h^{-1}$	$min.ha^{-1}$	$min.h^{-1}$	$min.ha^{-1}$
Grasslands	6.5	7	13.0	14	6.3	10	3.3	5
Moss dunes & open vegetation	0.3	0.4	2.3	2	11.0	10	5.3	5
Rough grasslands	1.5	2	7.3	10	5.2	9	3.7	7
Grassland with shrub invasion	3.3	5	5.7	8	1.2	4	1.3	5
Rough vegetation	2.0	2	4.5	5	1.7	5	8.2	13
Scrub	5.5	1.3	5.3	1.3	0.6	0.7	8.3	1
Woodland	3.8	3	4.2	3	7.3	5	0.7	0.5
GT in $min.h^{-1}$	22.9		42.3		33.3		30.8	

The introduced herbivores generally show a wide range of plant species in their diet. Observations on Konik ponies in the FNR Westhoek-north revealed that they ate of at least 114 plant species, Donkeys in the FNR Houtsaegerduinen consumed at least 138 different plant species (Hoffmann *et al.*, 2001; Cosyns *et al.*, 2001; Cosyns and Hoffmann, 2004; Cosyns, unpubl. data), Cattle in Westhoek-north ate from at least 104 plant species (Cosyns and Hoffmann, 2004), while Shetland ponies in Westhoek-south were seen biting at least 81 plant species (Goerlandt, 1999). Table IV mentions the 15 most frequently bitten plant species during the seed set period (May-October) by the respective herbivores grazing in the FNR Westhoek and Houtsaegerduinen. These numbers depend of herbivore specific preferences, but also on plant species availability.

Therefore, these figures do not allow to deduce diet preferences, since availability of the plant species at each of the sites is not known exactly. Neither do the figures tell us anything definite about the absolute impact on plant species. Rare species that are bitten only now and then will be heavily influenced by grazing (*e.g. Clematis vitalba)*, while very common species (*e.g.* most graminoids and woody plants mentioned in Table IV) are, in a relative sense, far less severely attacked. Above that, different plant species show different defence mechanisms against grazing. All herbivores are observed to bite graminoid species most frequently, with *Calamagrostis epigejos, Holcus lanatus, Carex arenaria, Festuca juncifolia* and *Poa trivialis* as leading victims.

Herbivore contribution to endozoochorous seed dispersal

138 plant taxa germinated from dung of Scottish Highland cattle, Galloway cattle, Haflinger pony, Konik pony, Shetland pony, Mergelland sheep, Donkey and Rabbit under greenhouse conditions (Table V). The total number of species that has ever been recorded to be dispersed (potentially) endozoochorously by Ungulate and Lagomorph species in temperate regions mounts up to 272 plant taxa (Cosyns, 2004). Data on epizoochory by donkeys as compared to endozoochory are given in Couvreur *et al.* (2005a, b) and are not treated here.

We notice that cattle, Konik ponies and sheep seem to be dispersers of larger amounts of plant species, while donkeys and rabbits might be less good dispersers. We should keep in mind though, that the total number of species depends on the quantity of seeds present at the sites, number of seeds consumed by the animals, herbivore-specific characteristics of the digestive system, number and volume of samples. Therefore, figures cannot be used reliably to compare individual herbivore species characteristics as vector for endozoochorous seed dispersal.

Table IV. The 15 most frequently bitten plant species per herbivore species in different nature reserves, during the period of seed set (May-October); data largely from Cosyns (2004) and Cosyns (unpubl. data). Ws: FNR Westhoek-south, Wn: FNR Westhoek-north; H: FNR Houtsaegerduinen; Herbivores: C: Scottish Highland Cattle; S: Shetland pony; K: Konik pony; D: Donkey. Figures represent % bites (*i.e.* the proportion of all bites taken from one plant species compared to the total number of bites (including the less frequently bitten plant species); it may concern bites of the entire plant, of leaves (by far the most frequent), stems, roots and rhizomes, inflorescences, fruits or litter

Site	Wn	Ws	Ws	Wn	H
Herbivore	C	C	S	K	D
Aegopodium podagraria		0,22			
Agrostis stolonifera	1,20		1,43	1,43	
Ammophila arenaria					2,08
Arenaria serpyllifolia				0,81	
Arrhenatherum elatius					4,62
Avenula pubescens					1,83
Betula pendula		0,26			
Bromus sterilis					7,42
Calamagrostis canescens	1,34			2,84	
Calamagrostis epigejos	9,27	3,40	8,52	**20,64**	9,67
Carex arenaria			0,75	0,59	**18,11**
Carex disticha			0,40		
Carex flacca				0,56	
Carex riparia		0,57			
Cerastium semidecandrum					2,54
Cirsium arvense			1,85	0,75	
Claytonia perfoliata	5,05		0,98	0,92	
Clematis vitalba		1,10			
Crataegus monogyna		0,76			
Elymus repens					2,60
Eupatorium cannabinum				1,06	
Festuca juncifolia					15,46
Festuca rubra			0,33		
Galium aparine	0,69				
Holcus lanatus	**20,99**	**24,20**	**17,91**	18,10	
Juncus bufonius	0,51		0,16	0,91	
Juncus inflexus			0,14		
Juncus subnodulosus	0,53	4,10	1,13	2,11	
Koeleria albescens					1,94
Ligustrum vulgare	0,98	0,30			
Lycopus europaeus	5,89				
Lythrum salicaria	1,44				
Phleum arenarium					2,31
Phragmites australis			0,16		

Site	Wn	Ws	Ws	Wn	H
Herbivore	C	C	S	K	D
Poa pratensis			1,36	0,71	1,38
Poa trivialis	16,49	19,30	1,26	11,93	1,52
Populus alba					1,95
Prunus spinosa		1,30			
Rosa pimpinellifolia		1,60			7,05
Rubus caesius	0,50	1,10	0,48	0,76	
Salix cinerea	1,08	0,37			
Salix repens		1,10			
Urtica dioica	2,13				

Table V Plant species of which seeds germinated from fresh dung samples of several Ungulate and one Lagomorph species from different sites at the Flemish Coast (samples collected during seven fortnightly sessions between 17 July and 10 October 2000; Claerbout, 2001), supplemented with observations by Cosyns (2004). Sampling sites: Ws: FNR Westhoek-south, Wn: FNR Westhoek-north; H: FNR Houtsaegerduinen; Y: FNR Ter Yde; IJ: FNR IJzermonding; He: FNR D'Heye; D: NR Doornpanne; G: NR Fossile dunes of Ghyvelde. Animals: Cattle: Scottish Highland Cattle (Ws and Wn) and Galloway (He); Horse: Haflinger pony (G), Shetland pony (Ws, D), Konik pony (Wn); Sheep: Mergelland sheep (IJ). *: species only mentioned to germinate from dung from the Flemish coastal dunes (Cosyns, 2004). Data adapted from Claerbout (2001) and Cosyns (2004)

	Animal species	Cattle	Donkey	Horse	Rabbit	Sheep
	Sites	Ws, Wn, He	H	G,Wn,Ws, D	G,D,IJ, Y	Y,IJ
	N (# dung samples)	34	14	58	22	20
	Total volume of dung	85 L	35 L	145 L	55 L	50 L
N°	Plant species					
1	*Achillea millefolium*	X	X	-	-	X
2	*Agrostis capillaris*	X	X	X	X	X
3	*Agrostis stolonifera*	X	X	X	X	X
4	*Aira praecox*	X	X	X	X	X
5	*Anagallis arvensis*	-	-	X	X	X
6	*Anchusa officinalis* *	-	-	X	-	-
7	*Anthoxanthum odoratum*	X	-	X	X	X
8	*Anthriscus caucalis*	X	X	X	X	X
9	*Aphanes inexpectata*	X	-	X	X	X
10	*Arabidopsis thaliana*	X	-	X	X	-
11	*Arenaria serpyllifolia*	X	X	X	X	X
12	*Artemisia vulgaris**	-	X	-	-	X
13	*Calamagrostis epigejos* *	X	X	X	X	X
14	*Calamagrostris canescens**	-	-	X	-	-
15	*Capsella bursa-pastoris*	X	X	X	X	X
16	*Cardamine hirsuta*	X	-	X	X	X
17	*Carex arenaria**	X	X	X	X	X

	Animal species	Cattle	Donkey	Horse	Rabbit	Sheep
	Sites	Ws, Wn, He	H	G,Wn,Ws, D	G,D,IJ, Y	Y,IJ
	N (# dung samples)	34	14	58	22	20
	Total volume of dung	85 L	35 L	145 L	55 L	50 L
N°	Plant species					
18	*Carex flacca**	X	-	X	-	X
19	*Carex trinervis**	-	-	X	-	-
20	*Carex viridula**	-	-	X	-	-
21	*Centaurium erythraea**	X	-	X	-	X
22	*Centaurium littorale**	X	-	X	-	X
23	*Cerastium fontanum*	X	X	X	X	X
24	*Cerastium semidecandrum*	X	-	X	X	-
25	*Chelidonium majus **	-	X	-	-	-
26	*Chenopodium album*	X	X	X	X	X
27	*Chenopodium murale**	-	-	X	-	X
28	*Chenopodium rubrum*	-	-	X	X	X
29	*Cirsium arvense*	X	-	X	-	X
30	*Claytonia perfoliata**	X	-	X	X	-
31	*Cochlearia danica**	-	-	X	X	X
32	*Conyza canadensis**	X	X	X	X	X
33	*Crepis capillaris*	X	X	-	X	X
34	*Cynoglossum officinale**	X	-	X	X	-
35	*Diplotaxis tenuifolia**	-	-	-	X	X
36	*Epilobium ciliatum**	X	X	X	-	-
37	*Epilobium hirsutum*	X	X	X	-	-
38	*Epilobium obscurum*	X	-	-	X	-
39	*Epilobium parviflorum**	X	-	X	X	X
40	*Epilobium roseum**	X	-	X	X	X
41	*Epilobium sp.*	X	X	X	X	X
42	*Erodium cicutarium/lebelii*	X	-	X	X	X
43	*Erophila verna*	X	-	-	X	X
44	*Eupatorium cannabinum*	X	X	X	X	X
45	*Fallopia convolvulus**	-	-	X	-	X
46	*Festuca arundinacea**	X	-	-	-	-
47	*Festuca filiformis**	-	-	X	-	X
48	*Festuca rubra*	X	X	X	X	X
49	*Galium aparine**	X	X	X	X	-
50	*Galium mollugo*	X	X	X	X	X
51	*Galium palustre*	X	-	X	-	-
52	*Galium uliginosum**	X	-	X	-	-
53	*Galium verum*	X	X	X	X	X
54	*Geranium molle*	X	X	X	X	X

	Animal species	Cattle	Donkey	Horse	Rabbit	Sheep
	Sites	Ws, Wn, He	H	G,Wn,Ws, D	G,D,IJ, Y	Y,IJ
	N (# dung samples)	34	14	58	22	20
	Total volume of dung	85 L	35 L	145 L	55 L	50 L
N°	Plant species					
55	*Geranium robertianum**	X	-	-	-	-
56	*Gnaphalium uliginosum*	X	-	X	-	X
57	*Helianthemum nummularium*	X	-	X	-	X
58	*Hieracium umbellatum**	-	-	-	-	X
59	*Holcus lanatus*	X	X	X	X	X
60	*Hydrocotyle vulgaris**	X	-	X	-	-
61	*Hypericum perforatum**	X	-	-	-	X
62	*Hypericum tetrapterum**	X	-	-	-	X
63	*Hypochaeris radicata**	-	X	-	X	-
64	*Juncus articulatus*	X	X	X	X	X
65	*Juncus bufonius*	X	X	X	X	X
66	*Juncus inflexus*	X	-	X	X	-
67	*Juncus subnodulosus**	X	-	-	-	X
68	*Koeleria albescens**	-	X	X	X	-
69	*Leontodon saxatilis**	-	X	X	X	X
70	*Lotus corniculatus*	X	-	X	-	X
71	*Lotus pedunculatus*	X	-	X	-	-
72	*Luzula campestris*	X	-	X	X	X
73	*Lychnis floscuculi**	X	-	-	-	-
74	*Lycopus europaeus*	X	-	X	-	X
75	*Lysimachia vulgaris**	X	-	X	-	-
76	*Lythrum salicaria**	X	X	X	-	X
77	*Matricaria matricarioides*	X	-	-	X	-
78	*Medicago arabica**	-	-	X	-	X
79	*Medicago lupulina*	X	X	X	-	X
80	*Medicago minima*	X	-	-	-	X
81	*Mentha aquatica**	X	-	X	-	X
82	*Mercurialis annua*	-	-	-	-	X
83	*Myosotis arvensis*	-	-	X	X	-
84	*Myosotis ramosissima**	X	-	X	X	X
85	*Oenothera glazioviana**	X	X	X	X	X
86	*Ononis repens**	X	-	X	-	X
87	*Ornithopus perpusillus*	.X	-	-	-	X
88	*Phleum arenarium*	-	-	-	X	X
89	*Phleum pratense**	X	X	X	X	X
90	*Plantago coronopus*	X	X	X	X	X
91	*Plantago lanceolata*	X	X	X	X	X

	Animal species	Cattle	Donkey	Horse	Rabbit	Sheep
	Sites	Ws, Wn, He	H	G,Wn,Ws, D	G,D,IJ, Y	Y,IJ
	N (# dung samples)	34	14	58	22	20
	Total volume of dung	85 L	35 L	145 L	55 L	50 L
N°	Plant species					
92	*Plantago major*	X	X	X	X	X
93	*Poa annua*	X	X	X	X	X
94	*Poa pratensis*	X	X	X	X	X
95	*Poa trivialis*	X	X	X	X	X
96	*Poa sp*	X	-	X	-	-
97	*Polygonum aviculare*	X	-	X	-	X
98	*Potentilla anserina**	X	-	X	-	-
99	*Potentilla reptans**	X	-	X	X	X
100	*Prunella vulgaris*	X	-	X	-	-
101	*Ranunculus bulbosus**	X	-	-	-	-
102	*Ranunculus repens*	X	X	X	-	X
103	*Ranunculus sceleratus**	X	-	X	-	-
104	*Ranunculus trichophyllus**	-	-	X	-	X
105	*Rubus caesius*	X	X	X	X	X
106	*Rumex acetosella*	X	-	X	X	X
107	*Rumex conglomeratus**	X	-	X	X	X
108	*Rumex crispus**	X	X	X	-	X
109	*Rumex obtusifolius*	X	-	X	X	X
110	*Rumex sp.*	X	-	X	-	X
111	*Sagina nodosa**	X	-	-	-	-
112	*Sagina procumbens / apetala*	X	X	X	X	X
113	*Samolus valerandi**	-	-	X	-	X
114	*Saxifraga tridactylites*	-	-	-	X	X
115	*Scirpus setaceus*	X	-	X	-	-
116	*Sedum acre*	X	-	X	X	X
117	*Senecio jacobaea*	X	X	X	X	X
118	*Senecio sylvaticus**	X	-	X	X	-
119	*Senecio vulgaris*	X	-	X	X	X
120	*Silene latifolia**	X	X	X	X	X
121	*Solanum dulcamara**	-	-	X	-	-
122	*Solanum nigrum**	X	X	X	X	X
123	*Sonchus asper*	X	-	X	X	X
124	*Sonchus oleraceus*	.X	X	X	X	X
125	*Stellaria graminea*	X	-	-	-	-
126	*Stellaria media*	X	X	X	X	X
127	*Taraxacum sp.*	X	-	X	-	X
128	*Trifolium arvense*	X	-	X	-	X

	Animal species	Cattle	Donkey	Horse	Rabbit	Sheep
	Sites	Ws, Wn, He	H	G,Wn,Ws, D	G,D,IJ, Y	Y,IJ
	N (# dung samples)	34	14	58	22	20
	Total volume of dung	85 L	35 L	145 L	55 L	50 L
N°	Plant species					
129	*Trifolium campestre*	X	-	X	X	X
130	*Trifolium dubium**	X	X	X	X	X
131	*Trifolium repens*	X	X	X	X	X
132	*Trifolium scabrum*	-	-	-	-	X
133	*Urtica dioica*	X	X	X	X	X
134	*Veronica chamaedrys+arven*	X	X	X	X	X
135	*Veronica officinalis*	X	-	X	X	-
136	*Veronica serpyllifolia*	X	-	X	X	X
137	*Vicia cracca**	-	X	X	-	X
138	*Viola curtisii**	-	-	X	-	-
	Total number of species	110	54	113	77	100

Evaluation: did grazers do what they were supposed to do?

Habitat use, forage behaviour and diet of introduced herbivores

Did they spare the vegetation that is vulnerable for trampling disturbance? Plant communities encountering a low foraging activity will not be influenced severely by the grazers. The impact can be expected to be highest in those vegetation types with an intensive grazing activity, not neglecting the fact that certain plant communities will be more vulnerable to the same amount of trampling, grazing or nutrient addition than others (*e.g.* the more vulnerable *Tortulo-Koelerion* (moss dunes) against the less sensitive *Polygalo-Koelerion* (dune grassland) within the *Cladonio-Koelerietalia*). In the Westhoek, moss dunes were not intensively used by ponies and cattle. Cattle foraged only in moss dunes in winter, ponies grazed there in winter and spring. Donkeys in the Houtsaegerduinen on the other hand, clearly foraged more in moss dunes, compared to the cattle and ponies in the Westhoek. However, we can reasonably assume that this grazing activity is not a threat for the moss dunes. The large herbivores move steadily while foraging, without disturbing the fragile moss layer. When the herbivores do not forage but travel through the moss dune, they use paths.

Did the herbivores have a strong impact on rough graminoid species, characterized by litter accumulation (*e.g. Calamagrostis epigejos* and *Holcus lanatus*) and did they influence scrub vegetation *through their habitat use?* Our results demonstrate that ponies (Shetland, Konik and Haflinger), cattle (Scottish Highlander) and donkeys are foraging predominantly in grass-dominated habitat and thus will have a relatively strong impact on this habitat. As a consequence of the vegetation selection within the grassy habitat not all distinguished grassy vegetation units will receive a similar grazing pressure. The large herbivores are foraging much less in scrub than in the grass-dominated habitat, and

therefore the grazing pressure and thus the grazing impact on scrub will be much lower. Of course, the relative area taken by the different vegetation types influences the amount of grazing impact on each of them. For example, grassland, foraged intensively by Shetland ponies and Highland cattle in Westhoek-south, takes a relatively small part of the total area, and thus the grazing pressure per ha grassland is high.
Although cattle and donkeys grazed considerable time in scrub and woodland, grazing pressure on these habitats remains very small since they cover a large part of the fenced areas. Cattle grazed almost as long in scrub (5.55min.h^{-1}) as in grassland (6.55min.h^{-1}), but the grazing pressure of cattle per ha scrub (0.22min.h^{-1}.ha^{-1}) is much lower than their grazing pressure per ha grassland (1.17min.h^{-1}.ha^{-1}). The same can be concluded for donkeys. Although they spent 16-27% of their grazing time in scrub, the grazing pressure per ha scrub is minimal (0.11-0.15min.h^{-1}.ha^{-1}). Because the donkeys initially did not move through the dense scrub to forage, their grazing activity in scrub was often limited to the edges of the scrub.

Did the herbivores have a strong impact through the diet selection? Important to predict the herbivore impact is not only the question 'where do they graze?', but also 'what do they eat?'. Cattle and donkeys only performed browsing activity when foraging in scrub, while Shetland ponies when foraging in scrub, only consumed graminoids and forbs there. In winter, Highland cattle and donkeys spent half of their grazing time in scrub (11.7min.h^{-1} and 15.8min.h^{-1}, respectively). These long grazing times in combination with the browsing activity implies that there are at least indications that cattle and donkeys can have a significant impact on scrub development. Scrub enlargement of *Ligustrum vulgare* and *Salix repens* is likely to be restrained by the browsing activity of donkeys and cattle, respectively, at least locally. *Hippophae rhamnoides*, which is considered as a problematic invasive shrub species, is browsed by cattle, but only occasionally consumed by donkeys (almost exclusively berries). Hence, in the Houtsaegerduinen, donkey introduction as only measure will not be sufficient to avoid further encroachment of *Hippophae rhamnoides*, as has been suggested by van Breukelen *et al.* (2002).
Calamagrostis epigejos is a graminoid species that is considered as a problematic dominant species and conservation management aims to prevent the further expansion of it. Data on the diet composition illustrate that *Calamagrostis epigejos* belongs to the most frequently foraged plant species; in case of the donkeys it forms even a major contribution to the diet. Since *C. epigejos* is a species which suffers from grazing, we can expect on the basis of our diet data that this species will decrea se in biomass and litter mass over time due to grazing. From 1998 to 2001, grazed plots that were initially dominated by *Calamagrostis epigejos* in Westhoek and Houtsaegerduinen showed a significantly decreased cover degree of *C. epigejos,* a decrease of litter cover and a significantly increased number of plant species, while the ungrazed control plots showed a significant cover increase of *C. epigejos* over the same period without significant change in number of plant species (Vervaet, 2002). Thus, the herbivores seem to be suitable to avoid further dominance of *C. epigejos*. A decrease in cover by *C. epigejos* was also found in Meijendel, a dune area in the Netherlands, grazed by ponies and cattle (de Bonte *et al.*, 1999). The lower cover of *C. epigejos* creates the possibility for other plant species to germinate and establish (see below).

Does the habitat and diet selection create spatial heterogeneity? Another aspect of the grazing behaviour of large herbivores is the terrain use, *i.e.* the way the herbivores use the (theoretically) available space. It is typical of grazing management in heterogeneous landscapes that some sites are intensively grazed by the herbivores, while others are hardly ever visited. Consequently, some sites experience a high grazing pressure and are thus intensively 'managed', and others receive no or 'less' management. In the Westhoek, foraging behaviour of the cattle is more distributed over the entire fenced area, while the foraging behaviour of the ponies was concentrated in particular areas. One central grass-dominated patch in the Westhoek counted 27.8% of the cattle location observations and 54.3% of the pony location observations. Consequently, the impact of grazing by cattle will be more distributed, while the grazing pressure of the ponies will be more aggregated. Similarly, Vulink (2001) found that Konik ponies concentrated on short grassland for most of the year, while cattle foraged more evenly dispersed all over the available space (Oostvaardersplassen, the Netherlands). If ponies would be the only large herbivores in the Westhoek, it would be very probable that smaller grass-dominated patches enclosed by scrub, would not be 'managed' at all. In that case, invasion of competitive grass and shrub species into these patches would not be hampered. Although the terrain use of donkeys in the Houtsaegerduinen is not concentrated at one specific site, some parts of the area encounter a higher grazing pressure than others. Closed scrub covers large parts of the reserve and, similarly to the ponies, the donkeys initially did not forage in or move through these scrubs. Later (after several years) they gradually explored the scrub area and created small paths that enabled them to graze grass-dominated islands within the scrub.

Does defecation behaviour influence spatial heterogeneity? Nutrient transfer is often mentioned as one of the possible impacts of grazing management. A depletion of nutrients would occur in the preferred grazing sites, whereas areas with faeces concentration would show an accumulation of nutrients, especially in nutrient-poor systems. Such a nutrient transfer is found in areas grazed by sheep (Bakker *et al.*, 1983) and cattle (Bokdam and Gleichman, 2000; Bokdam, 2003). According to our observations (Lamoot *et al.*, 2004a), we can state that this process is not likely to occur on a large scale in nature reserves grazed by equids. Since we found that the equids under consideration generally defecate where they graze, they do not relocate nutrients between different habitats. Patches with highest grazing pressure will receive a proportional concentration of faeces and urine.

Seed dispersal and its conservation interest

Cattle, horse breeds, donkeys, sheep and rabbits all appear to be potentially highly relevant dispersal agents for a wide variety of plant species in the coastal dunes. It was shown that they are able to disperse large amounts of viable seeds, including seeds of plant species that are of conservation interest. However, probably due to the low abundance of these plant species in vegetation, only low numbers of species and small amounts of viable seeds were recorded from dung. Out of the 107 Flemish red list species, that were found in all study sites together, only 11 species occurred from dung samples. A higher proportion of nature conservation target species (as defined by

Provoost and Hoffmann, 1996) that are known from the study sites (*i.e.* red list and characteristic species) were recorded from dung, *i.e.* 36 out of 143 plant species.
Within the structurally heterogeneous coastal dune landscape the potential long-distance seed dispersal capacity of ungulates may enhance intra and inter habitat seed dispersal, *e.g.* between species poor *Calamagrostis* dominated grassland and species rich dune grassland.
Considering the number of grazing animals, their defecation frequency and habitat use and the amount of viable seeds of target species found in their dung, an estimate can be given of the amount of target species that could possibly be introduced in species poor *Calamagrostis* dominated grassland by ungulates. Within Westhoek-south, endozoochory could contribute to potential seed dispersal of 10 out of the 30 target species of dune grassland. However, because of the observed interspecific differences in seedling densities, arrival time and subsequent establishment will most probably differ between plant species. If all areas of the Westhoek would be included in one large grazed block, two more plant species can be expected to get endozoochorously dispersed and hence possibly get deposited in target areas, such as *Calamagrostis epigejos* dominated grassland and deforestation areas. It was already shown that grazing activity helps to open the initially very dense *Calamagrostis* sward, enabling new species to arrive, germinate and establish. Whether other target species will ever arrive at target areas and by what means, remains highly speculative. Wind, could be one of the most plausible dispersal agents, but anemochory is generally an overestimated long-distance seed dispersal modus (Soons, 2003).
Since large herbivores have always been part of natural ecosystems, their role as epi- and endozoochorous dispersal vectors is probably indispensable for maintaining species richness. Grazing, being an important nature management tool for conservation and restoration of many habitats in northern temperate regions, obtains therefore an additional argument. Until now, much attention was given to the contribution of livestock to diversity of vegetation structure and plant and animal diversity patterns, both at the local and the landscape scale, through their activities of selective grazing, trampling and defecating (recent review in Cosyns and Hoffmann, 2004). But herbivores will also influence plant diversity through processes that affect colonisation rates (Olff and Ritchie, 1998). Our results clearly show the importance of large herbivores as (long-distance) seed dispersal vectors for many more plant species, than could be assumed from the morphological dispersal adaptations of seeds. The growing evidence of the role that large herbivores can play in the seed dispersal process, urges for a well-considered nature management policy that 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 or other large herbivores as managers might help to reach this goal, through the epi- and endozoochorous dispersal of seeds (see also Couvreur *et al.*, 2005).

General conclusions

We have many reasons to state that the introduced ungulates in coastal dunes contribute substantially to the initial management goals. They will certainly diminish dominance of

rough, litter accumulating gramonoid species like *Calamagrostis epigejos, Holcus lanatus, Arrhenatherum elatius, Carex arenaria* and others, enabling target species of dune grassland (*Polygalo-Koelerion*) to colonize gaps in the grassland sward. We further believe that endozoochorous dispersal will have an accelerating effect on target species arrival in gaps in monospecific grass-dominated habitats, gaps that most likely will have been created by grazer activity.
Impact of grazers on scrub encroachment, let alone scrub decrease, will be far less important, although Scottish Highland cattle will have a relevant impact on scrub structure and, in the end, scrub area. The horse breeds only seem to act as followers, after cattle has created gaps in the scrub; donkeys appear to act intermediate between cattle and horse breeds. Together with cattle, they show quite some browsing activity, but they hardly ever take initiative to penetrate closed canopy scrub.
It remains to be studied what contribution is added by sheep grazing. Some preliminary results of permanent plot research in the FNR de IJzermonding, points out that, within a dune grassland environment, rough grass and litter cover diminishes under sheep grazing, while total number of species increases (Hoffmann *et al.,* 2004). Research on how they interact with tidal marsh vegetation is still in progress.
Further research remains to be done on the carrying capacity of the relatively low productive coastal dune areas, since year round grazing puts (temporary) severe pressure on primary production. Some areas might well be overgrazed on the long run, when maintaining herds with 75-95 $kg.ha^{-1}$, as is the case in Westhoek-south. Further enlargement of grazed area would further differentiate grazing activity and impact, but will simultaneously increase the unpredictability of the outcome of the grazing management.

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