

Habitat use of ponies and cattle foraging together in a coastal dune area

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Abstract

Grazing by large ungulates has been chosen as a management tool in scrub-dominated dune reserves at the Belgian coast. Due to morphological and physiological differences between cattle and ponies, differences in foraging behaviour and habitat use are expected, and these may result in a different impact on the spatially heterogeneous and nutrient-limited ecosystem. Grazing behaviour and habitat use of Shetland ponies and Highland cattle, grazing together in a coastal dune area (60 ha) were investigated at various levels of the foraging hierarchy (habitat, vegetation type, sward height and diet). Habitat use overlap was high in all seasons; both cattle and pony spent most of their grazing time in the grass-dominated habitat. However, Shetland ponies concentrated their grazing activity more on the grass-dominated habitat than did cattle. Cattle spent a greater proportion of their grazing activity in woodland and scrub, compared to the ponies. Foraging activity in woodland and scrub is strongly influenced by season. Within the grass-dominated habitat both species preferred foraging in the grasslands and avoided open vegetation and moss dunes. Within the grasslands, cattle grazed less on the short swards than did ponies. Both cattle and ponies predominantly foraged on graminoids, though there are minor differences between both species and among seasons. Browsing of woody plants occurred only by cattle. Where grazing management has been implemented to maintain dune grasslands and to avoid further invasion by scrub, a combination of cattle and ponies appears to be adequate. Ponies are suitable for maintaining grasslands, but they have no impact on invading scrub. Cattle have an impact on scrub development, both by direct consumption of various shrub species and by opening initially closed scrub.

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1. Introduction

In the late 1990s different species of domesticated large herbivores were introduced in several dune reserves along the Belgian coast, to avoid further expansion of dominant grasses and woody plants. Until the twentieth century practically all coastal dunes were

grazed as an agricultural practice, but only recently a number of dune areas have again been designated for management by grazing (Piek, 1998), in the Netherlands as well as in Belgium. However, only a few studies deal with free-ranging herbivores in this heterogeneous but relatively nutrient-poor dune system (Cosyns et al., 2001; Hoffmann et al., 2001). In addition, there is a lack of information for the management of several species of large herbivores coexisting in this type of ecosystem. The large herbivores have to deal with a heterogeneous area, differing spatially and temporally in forage quality, quantity and structure. Free-ranging herbivores have

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to make many foraging decisions at different resolution levels (Senft et al., 1987; Stuth, 1991), resulting in a foraging strategy that meets the large herbivores' nutrient and energy requirements. Habitat use is an outcome of the foraging strategy of the herbivores; it is the expression of the way grazing animals resolve the conflict between their need for food and their intrinsic and extrinsic constraints (Illius and Gordon, 1993). Coexisting ungulates tend to use their environment in different ways (Gordon, 1989b), resulting in 'niche differentiation' or 'resource partitioning'.

Our study animals, Shetland ponies and Highland cattle, differ in many aspects which may result in a differential use of their environment, and therefore in varying impacts on the vegetation. Digestive system (Bell, 1971; Janis, 1976; Rittenhouse, 1986), body size (Van Soest et al., 1983), structure of the incisor arcade (Gordon and Illius, 1988), metabolic requirements (Rittenhouse, 1986) are some of the characteristics differing largely between bovids and equids. Cattle, being ruminants, and ponies, being hindgut fermenters, extract the nutrients of the consumed food items in a different way. Cattle digest the cell wall fractions more completely than equids, but achieve a smaller intake rate because the forage is retained for a longer period in the digestive tract. Equids on the other hand can have higher intake rates enabling them to reach a high rate of nutrient extraction on a daily basis as well (Rittenhouse, 1986; Duncan et al., 1990). Illius and Gordon (1992) reported that the more efficient digestion by ruminants would give them advantage over the equids, only when food quantity is limited and food intake is restricted. Plant secondary compounds are (partly) detoxified by the rumen flora of cattle and this might be a more important advantage of cattle compared to equids (Duncan et al., 1990). Irrespective of the digestive system, smaller animals (e.g. Shetland ponies) have relatively larger energy requirements than larger animals (e.g. Highland cattle) (Demment and Van Soest, 1985; Illius and Gordon, 1987). Small animals may be 'forced' to select more for quality, while larger animals may be less selective and search for quantity. In addition, larger herbivores have larger mouth parts and are therefore unable to forage with a high degree of selectivity compared to smaller herbivores (Illius and Gordon, 1990). Besides these morphological and physiological differences, both cattle and horses are known generally as bulk feeders, consuming large quantities of forage of low to medium quality. They preferentially graze in grass-dominated vegetation types (Duncan, 1983; Pratt et al., 1986; Putman et al., 1987; Gordon, 1989a; Menard et al., 2002) and graminoids form the main part of their diet (Van Dyne et al., 1980).

The aim of the present study is to determine the differences in grazing behaviour and habitat use of a herd of Shetland ponies and a group of Highland cattle graz-

ing together in a fenced part (ca. 60 ha) of the 'Westhoek' dune nature reserve at the Belgian coast. The differences in habitat use of both species are investigated at various foraging scales. We examine to what extent niche differentiation occurs at the level of (i) the habitat type (grassy habitat, scrub and woodland), (ii) the vegetation units within the grassy habitat, (iii) the sward height within the preferred vegetation unit, (iv) the consumed forage classes. Because the Westhoek reserve is a relatively nutrient poor ecosystem (unpubl. data Co-syns) with a high animal biomass density (compared to near-natural grazing systems in the temperate regions (WallisDeVries, 1998)), we expect niche differentiation between the ponies and cattle to occur at least at one of these foraging levels (Pratt et al., 1986; Gordon, 1989a; Menard et al., 2002). If both species forage in the same habitats, we hypothesize that they select niches with a different species composition and/or sward height. It has been suggested that cattle are unable to graze very short swards due to their mouth morphology (Illius and Gordon, 1987), thus we expected the cattle to avoid grazing the short sward heights. We hypothesized that dicotyledons would be more consumed by the cattle than by the ponies, since cattle are able to detoxify secondary plant compounds (much commoner in dicotyledons) (Freeland and Janzen, 1974), which is unknown for equids.

2. Methods

2.1. Study area and animals

The "Westhoek" nature reserve (total area 340 ha) offers a diverse landscape consisting of a fore dune ridge and two dune slack zones that are separated by a large mobile dune. "Westhoek-South" (ca. 60 ha), a fenced area in the south of the "Westhoek" is grazed by 20–29 Shetland ponies and four Highland cattle. The area includes a dune slack zone and an inner dune ridge. Approximately 41% of this area is covered by more or less closed scrub vegetation: main shrub species are *Hippophae rhamnoides*, *Ligustrum vulgare*, *Salix repens*, *Crataegus monogyna* and *Prunus spinosa*. Woodland forms another main part of the area (approximately 14%): tree species are *Populus tremula*, *Populus x canadensis*, *Populus canescens*, *Ulmus minor* and *Alnus glutinosa*. The rest of the fenced area (45%) is occupied by grassy habitat. Within the grassy habitat we distinguished the vegetation units 'grasslands', 'rough grasslands', 'grasslands with scrub invasion', 'rough vegetation' and 'moss dunes and open vegetation'. Dry dune grasslands with *Poa pratensis*, *Avenula pubescens*, *Veronica chamaedrys*, *Galium verum* are part of the 'grassland' unit, as well as the moist *Holcus lanatus* grasslands with small forbs like *Prunella vulgaris*. The

vegetation unit ‘rough grasslands’ is the assembly of species-poor dry grasslands dominated by *Calamagrostis epigejos* and wet patches occupied by *Juncus subnodulosus* whether or not accompanied by *Lysimachia vulgaris*, *Lythrum salicaria* or *Mentha aquatica*. Due to the encroachment of invasive shrub species some grassland entities evolved into more scattered grassy patches with young scrub of mainly *Hippophae rhamnoides*, *Ligustrum vulgare* or *Salix repens*. Rough vegetation is characterized by tall forbs such as *Eupatorium cannabinum*, *Cirsium arvense*, *Lythrum salicaria* and *Iris pseudacorus*. Vegetation entities formed by *Rosa pimpinellifolia* are also classified as ‘rough vegetation’. Mosses and lichens are the dominant species of moss dunes. Main species of open vegetation are *Carex arenaria*, *Festuca juncifolia* or *Ammophila arenaria*.

Seven Shetland ponies and two Highland cattle were released, in 1997 and 1998, respectively, as a nature management measure in “Westhoek-South”. The animals are free-ranging and remain in the area year round. They receive no additional food. The herds are managed to avoid inbreeding and overgrazing. During the study period (August 2001–March 2002) the group of Highland cattle consisted of one cow and three bulls (two of them are offspring of the cow). We have no weight data from this group of cattle, though we have weight data from another group of Highland cattle, grazing in “Westhoek-North”; mean weight of the cows is 481 ± 21 kg, mean weight of the bulls is 520 ± 43 kg. Composition of the herd of Shetland ponies changed during the study period. In August 2001, 29 ponies grazed in the reserve: 15 females (10 lactating mares, two non-lactating mares and three fillies) and 14 males (one dominant stallion, four geldings, two yearlings and seven colts). In October 2001, nine ponies were removed: four lactating mares with their foals, one non-lactating mare and one gelding. Mean weight of the mares is 205 ± 8 kg; mean weight of the stallions is 174 ± 9 kg. Animal biomass during the study was high ($85\text{--}107$ kg ha⁻¹) compared to the range of biomass in near-natural grazing systems in temperate regions ($8\text{--}67$ kg ha⁻¹) (WallisDeVries, 1998).

2.2. Behavioural observations

Observational data were collected through continuous focal animal sampling (Altmann, 1974) from August 2001 until March 2002. During a 6-h period (daylight, ranging from 5.30 h until 22.30 h) we continuously monitored the behaviour of a focal animal, chosen at random from a pool of possible study animals before the start of an observation session. We recorded, on a protocol form, the start and end time (accuracy: 1 s) of the observed behaviours, as well as the vegetation type and sward height in which the behaviours were performed. When the focal animal was grazing, we recorded plant

species eaten and the number of bites taken (using a mechanical counter). Every 15 min the position of the focal animal was marked on an infrared aerial photograph (1/2000) (EUROSENSE, flight date: 1998). Most of the study animals were habituated to the presence of humans and could be approached closely (1 m) without obvious influence on their behaviour. During each observation period we observed either ponies or cattle, the other species was observed during the following session. We tried to minimize the time between observations of the two species. On average there were three days between the 6-h observations of both species. All cattle individuals were included in the observations, while six adult mares were included in the case of the ponies. Season definition follows the plant productivity periods in temperate regions, i.e. summer (June–August), autumn (September–November), winter (December–February) and spring (March–May). For each species 30 observation periods were performed: six in summer, twelve in autumn, eight in winter and four in spring.

The different vegetation types distinguished in the field were grouped into three habitat types: ‘woodland’, ‘scrub’ and ‘grassy habitat’, with the latter consisting of five vegetation units: ‘grasslands’, ‘rough grasslands’, ‘grasslands with scrub invasion’, ‘rough vegetation’ and ‘moss dunes and open vegetation’ as described above. To determine sward height in the field we used a scale related to the animal’s physiognomy: ‘no height’ (in case of no vegetation), ‘shortly grazed’, ‘hoof’, ‘knee’, ‘belly’, ‘spine’ and ‘higher’. For the present study we retained only ‘shortly grazed’, ‘hoof’ and ‘knee and higher’ which corresponds with ‘<3 cm’, ‘3–20 cm’ and ‘>20 cm’, respectively. All plant species eaten were grouped into four forage classes: ‘graminoids’ (grasses, sedges and rushes), ‘forbs’, ‘woody plants’ and ‘other’ (including mosses and ferns, unidentified plant species, soil).

2.3. Data analysis and statistics

To analyse the differences in grazing behaviour between the two species, we investigated the grazing variables ‘proportion of time spent grazing’, ‘number of bites taken’ and ‘bite rate’ (number of bites/minute grazing). These grazing variables were calculated per day. We used mixed-models ANOVA to investigate the effects of the fixed factors Species and Season and the interaction Species $\times$ Season on the variation in proportion of time spent grazing, number of bites and bite rate. We included the factor Season because we expected seasonal differences in the grazing behaviour. In addition, differences in grazing behaviour may exist between individual animals; therefore we initially included the random factor ‘Individual’ in our ANOVA model. A repeated statement was used to take into account the fact that the individual animals were sampled more than

once. If the random factor was not significant, we excluded it from the final model. Similarly, we eliminated non-significant interactions of the fixed effects from our ANOVA model.

We investigated the feeding niches of the herbivores at different levels. Firstly, how do the herbivores spread their grazing activity among the three habitat types, i.e. grassy habitat, scrub and woodland? Secondly, when grazing in the grassy habitat how do they partition their grazing activities among the five distinguished vegetation units (grasslands, rough grasslands, grasslands with scrub invasion, rough vegetation and open vegetation)? Thirdly, do they graze in different sward heights when foraging in intensively used vegetation units? Finally, we examined differences in diet composition. The grazing variables are: 'proportion of grazing time', 'proportion of bites taken' and 'bite rate'. For the calculation of the proportion of grazing time and the proportion of bites taken in the different habitat types, vegetation units, sward heights or forage classes we included zero values when on a given day an animal did not graze in a given habitat type (or vegetation unit or sward height or forage class). This is appropriate because we assume that an animal can graze potentially in all habitat types (or vegetation units or sward heights or forage classes) within a 6-h observation period. We did not include zero values for the calculation of bite rate in the different habitat types (or vegetation units or sward heights). Consequently, we examined the effective bite rate. The variation in the three grazing variables was examined with a mixed-model ANOVA. Fixed factors were Habitat (or Vegetation unit or Height or Forage Class), Species, Season and all their interactions. Again the random factor Individual was included in the model, as well as the repeated statement.

The positional data collected every 15 min during a 6-h period made it possible to calculate the cumulative distance travelled per observation session. We analysed whether this travel distance was different between both species and among seasons, using an ANOVA-model.

Data which are proportions were arcsin transformed; other data were logarithmically transformed. Analyses of variance were performed using SAS System V8. Number of degrees of freedom was estimated by the Satterthwaite-method. The positional field data were digitalised and processed with ArcView GIS 3.2a.

To quantify habitat preference, we used Jacobs' (1974) index of selection that takes into account the availability of the different habitat types:

$$D_i = (p_i - A_i) / ((p_i + A_i) - (2 \times p_i \times A_i)),$$

with p_i the mean proportion of the total grazing time spent in the i th habitat type and A_i the proportion of the area covered by the i th habitat type. The value of D ranges from -1 to $+1$, with negative and positive val-

ues indicating avoidance and selection, respectively, of the habitat type.

We also quantified habitat niche breadth and habitat overlap to estimate the width of habitat use and the intensity of habitat overlap, respectively. As the niche breadth index we applied Simpson's diversity index ($D = 1 / \sum p_i^2$) (Begon et al., 1996), which was originally employed to measure the species diversity of a system and was used by Menard et al. (2002) to reflect how "diverse" the habitat use of the herbivore species was. We choose Kulczynski's index (α_{hc}) (Oosting, 1956) to measure niche overlap. $\alpha_{hc} = \sum \min(p_{ip}, p_{ic})$ where p_{ip} and p_{ic} are the proportions of the grazing time that ponies and cattle, respectively, spent in the i th habitat type (or vegetation unit or sward height). We also employed these indices to examine forage niche breadth and forage use overlap, with p_i being the proportion of the total number of bites taken in the i th forage class.

3. Results

3.1. Grazing behaviour of cattle and ponies

The proportion of time spent on grazing was significantly affected by the factors Species ($F_{1,8.22} = 30.55$; $P < 0.001$) and Season ($F_{3,48} = 3.75$; $P = 0.017$). Ponies spent more time grazing than cattle (Table 1). Both species had significantly higher grazing times in winter than in summer. The number of bites taken was different between species ($F_{1,7.88} = 15.32$; $P < 0.001$), but not among seasons. Ponies took significantly more bites than cattle. Ponies and cattle had similar bite rates, but in both species the bite rate was influenced by Season ($F_{3,47.5} = 3.61$; $P = 0.020$). Both herbivores had a significantly higher bite rate in spring as compared to winter. The interaction between species and season was not significant for the three variables. Some of the variation in the proportion of time spent on grazing could be explained by the variation between individual animals within species (i.e. the random factor).

3.2. Habitat use

3.2.1. Selecting between grassy habitat, scrub and woodland

Both species divided their grazing time and their bites disproportionately among the different habitat types, as the variables 'proportion of grazing time' and 'proportion of bites' were significantly affected by Habitat (Table 2). In addition, the interactions Habitat $\times$ Species and Habitat $\times$ Season were significant. Both species spent most of their foraging activity in the grassy habitat, although the interaction Habitat $\times$ Species shows that there existed a difference between both species.

Table 1
Grazing behaviour of cattle and ponies throughout the year and in the different seasons

		% of time	Bites	Bite rate
Cattle	Year	38.4 ± 5.8	4215 ± 1096	29.2 ± 4.6
	Summer	30.2 ± 5.4	3404 ± 887	30.5 ± 5.2
	Autumn	37.9 ± 2.1	4310 ± 498	31.6 ± 3.3
	Winter	46.2 ± 6.6	4015 ± 1155	21.9 ± 4.4
	Spring	39.2 ± 9.3	5130 ± 1842	32.7 ± 5.4
Ponies	Year	70.7 ± 5.2	8031 ± 755	31.5 ± 2.0
	Summer	65.9 ± 7.7	6570 ± 813	27.7 ± 1.8
	Autumn	69.3 ± 2.8	7330 ± 482	29.5 ± 1.7
	Winter	75.1 ± 3.2	7489 ± 735	27.5 ± 2.2
	Spring	72.6 ± 7.1	10733 ± 990	41.2 ± 2.2

Mean values per 6-h period ± SE. % of time: proportion of time spent on grazing.

Table 2
Results of the ANOVA-model examining the effects of the factors Habitat, Species and Season on the variables 'proportion of grazing time', 'proportion of bites' and 'bite rate'

	df ₁	Grazing time			Bites			Bite rate		
		df ₂	F	P	df ₂	F	P	df ₂	F	P
Species	1	85.3	0.01	0.913	7.53	0.00	0.979	53.2	10.50	0.002
Season	3	101	0.25	0.862	97.2	0.15	0.929	61.3	4.35	0.008
Habitat	2	156	92.72	<0.001	27.6	97.25	<0.001	79.5	23.61	<0.001
Species × Season	3			n.s.			n.s.			n.s.
Species × Habitat	2	157	11.25	<0.001	21.8	6.42	<0.001	79.5	23.61	<0.001
Habitat × Season	6	156	11.47	<0.001	136	11.03	<0.001			n.s.
Species × Habitat × Season	6			n.s.			n.s.			n.s.

Non-significant 3-way and 2-way interactions were eliminated from the final model.

Ponies spent a bigger proportion of their grazing time in grassy habitat than cattle (grassy: P (ponies): 79%, C (cattle): 55%), while the cattle spent a bigger proportion of their grazing time in both scrub and woodland compared to the ponies (scrub: P: 12%, C: 26%; woodland: P: 9%, C: 19%). The same trend is found for the proportion of bites taken in the three habitat types (grassy: P: 82%, C: 62%; scrub: P: 10%, C: 22%; woodland: P: 8%, C: 16%). The interaction Habitat × Season indicates that the habitat use changed throughout the year (Fig. 1). In all seasons the grassy habitat was a intensively foraged habitat, but seasonal shifts are notable for scrub and woodland. In autumn and especially in winter, scrub was grazed often by both species, while it was the least grazed habitat type during spring. Woodland belonged to the most grazed habitat types in spring (cattle even foraged more intensively in woodland than in grassy habitat in spring), while it was much less grazed in the other seasons.

Calculating the Jacobs' index for selection, which takes into account the availability of the different habitat types, shows us whether the habitat types/vegetation units were selected or avoided (Table 3). Throughout the year, woodland was preferred by cattle and avoided by ponies. However, calculated by season, woodland was only preferred in spring, and this by both species. Scrub covers a large area of the nature reserve (41%) and

although scrub was grazed intensively in winter, we could not conclude that it was a preferred habitat in winter.

We examined the effective bite rate per habitat type and found a significant effect of the main factors Species, Habitat and Season and of the interaction Habitat × Species (Table 2). Both species had similar bite rates when foraging in grassy habitat, but ponies grazed faster than cattle in scrub and woodland.

3.2.2. Selecting vegetation units within the grassy habitat

Both species concentrated their foraging in the grassy habitat, though it was possible that they divided their foraging activity differently over the distinguished vegetation units within this habitat type. The results of ANOVA show that the factor Vegetation Unit ($F_{4,186} = 12.45$; $P < 0.001$) and the interaction Vegetation Unit × Season ($F_{12,188} = 3.94$; $P < 0.001$) had significant effects on the proportion of grazing time. Similar results were found for the analysis on the variable 'proportion of bites': significant effect of Vegetation Unit ($F_{4,184} = 13.52$; $P < 0.001$) and significant interaction Vegetation Unit × Season ($F_{12,187} = 3.50$; $P < 0.001$). Fig. 2 illustrates the proportion of grazing time spent in the five vegetation units when grazing in grassy habitat. Both species divided their grazing activity not uniformly over the five vegetation units, and this habitat

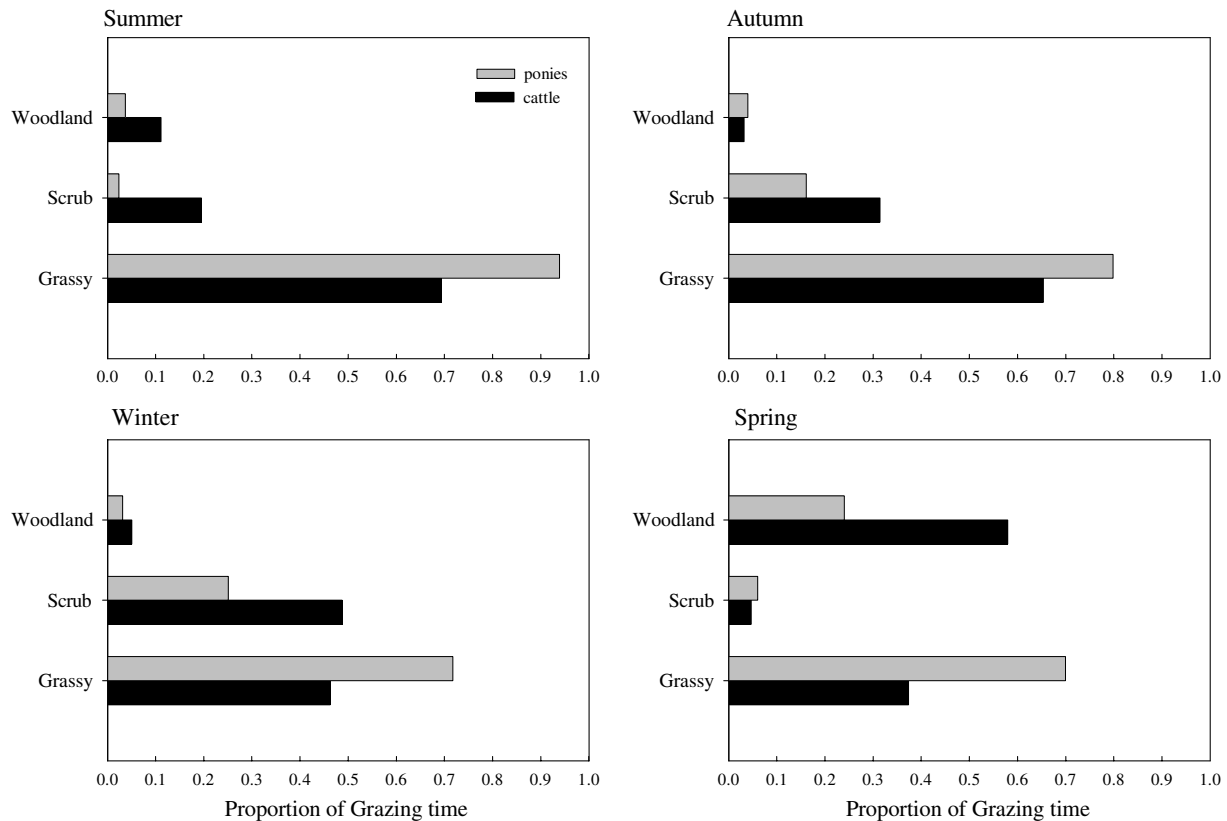


Fig. 1. Habitat use of cattle and ponies in the different seasons: the proportion of grazing time spent in the three habitat types.

Table 3
Jacobs' index of selection for cattle (C) and ponies (P)

Habitat type/vegetation unit	Area	Year		Summer		Autumn		Winter		Spring	
		C	P	C	P	C	P	C	P	C	P
Grassy: grasslands	9%	++	++	++	++	++	++	+	++	++	++
Grassy: moss dunes and open vegetation	11%	--	--	--	--	--	--	--	0	--	0
Grassy: rough grasslands	8%	-	-	++	++	+	+	--	--	--	--
Grassy: grasslands with shrub invasion	7%	+	+	++	+	+	++	++	+	--	+
Grassy: rough vegetation	9%	0	0	0	--	0	0	-	++	0	0
Scrub	41%	-	-	--	--	-	--	0	-	--	--
Woodland	14%	+	-	0	--	--	--	--	--	++	++

No selection (0): $-0.08 < \text{index} < 0.08$. Avoidance (-): $-0.4 < \text{index} < -0.08$. Strong avoidance (--): $\text{index} < -0.4$. Preference (+): $0.08 < \text{index} < 0.4$. Strong preference (++): $\text{index} > 0.4$.

use was also variable over the seasons. Slight differences between both species are visible, but these are not significant. In all seasons the grasslands were grazed intensively. Other vegetation units were more or less foraged depending on the season. For example, rough grasslands were not grazed in winter and spring, but were grazed in summer and autumn, which is also reflected in the Jacobs' index of selection (Table 3). The opposite trend is visible for open vegetation and moss dunes, although this vegetation type was never a 'preferred' vegetation.

The bite rate was significantly affected by the factors Vegetation Unit ($F_{4,143} = 2.97$; $P = 0.022$) and Season

($F_{3,90.6} = 4.95$; $P = 0.003$) and by the interaction Vegetation Unit $\times$ Season ($F_{12, 144} = 2.23$; $P = 0.016$). Thus, the bite rate depended on the grazed vegetation unit, with in general highest bite rates in grassland and in rough vegetation. The significant interaction illustrates however that this varied among seasons. The trends were similar for both species.

3.2.3. Foraging in commonly used vegetation units

When the two species foraged in the same vegetation units, it was possible that they differentiated their resource use by exploiting different sward heights. We

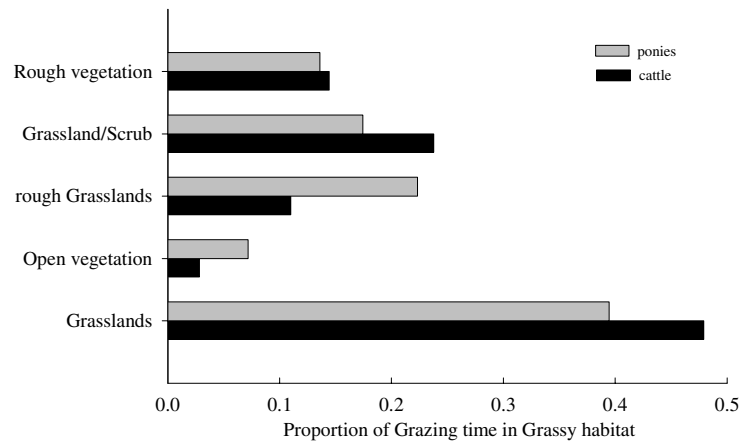


Fig. 2. The proportion of grazing time spent in the five vegetation units within the habitat type 'grassy habitat', averaged over the four seasons.

investigated this in the grasslands, a vegetation unit which was highly preferred by both cattle and ponies (Fig. 2; Table 3). The results of the ANOVA (Table 4) show that the proportion of the grazing time was significantly affected by the factor Height, indicating that grazing time was not divided uniformly over the different sward height categories. Moreover the pattern was influenced by Species and by Seasons, as demonstrated by the significant interactions Height $\times$ Species and Height $\times$ Season. Throughout the year, when grazing in grassland, both species spent very little time grazing in swards of more than 20 cm, as compared to the shorter swards. Nevertheless, there is a clear seasonal influence, as in summer the swards of more than 20 cm are grazed in a similar proportion as the swards of less than 3 cm. The significant interaction Height $\times$ Species shows that both species used the different sward heights in a different way. Ponies spent similar proportions of their grazing time in swards of less than 3 cm and in swards of 3–20 cm, while cattle spent more time grazing in swards of 3–20 cm, than in swards of less than 3 cm (Fig. 3). We found the same results when we considered the variable 'proportion of bites' (Table 4).

When grazing in grasslands cattle achieved a higher bite rate than ponies (40 and 31 bites/min, respectively), as indicated by the significant effect of the factor Species on 'bite rate' (Table 4). There were also significant effects of the factors Height and Season, and of the interaction Height $\times$ Season. Overall, the herbivores had highest bite rate when grazing in a sward of less than 3 cm, but this was variable among seasons.

3.3. Diet composition

Table 5 shows the plant species from which more than 500 bites were taken during the 30 sessions of six observation hours per herbivore species. It is obvious that both cattle and ponies foraged mainly on graminoids. The total diet of cattle consisted of 10 species of graminoids, 23 species of forbs and 17 woody plant species; that of the ponies consisted of 15 species of graminoids, 41 species of forbs and 9 species of woody plants. The number of graminoids species is probably underestimated, because the 'mix of graminoids' supposedly contains additional species such as small *Poa* species. We investigated the differences in diet composition of cattle and ponies at several levels.

Table 4

Results of the ANOVA-model examining the effects of the factors Height, Species and Season on the variables 'proportion of grazing time', 'proportion of bites' and 'bite rate', when the grazers were foraging in grasslands

	df ₁	Grazing time			Bites			Bite rate		
		df ₂	F	P	df ₂	F	P	df ₂	F	P
Species	1	58.6	0.02	0.895	57.6	0.00	0.953	32.4	6.7	0.014
Season	3	66.3	0.06	0.983	65.4	0.05	0.985	55.4	8.02	<0.001
Height	2	117	27.63	<0.001	116	26.58	<0.001	73.2	11.12	<0.001
Species $\times$ Season	3			n.s.			n.s.			n.s.
Species $\times$ Height	2	128	9.02	<0.001	128	10.37	<0.001			n.s.
Height $\times$ Season	6	124	5.62	<0.001	124	4.84	<0.001	71.3	4.59	<0.001
Species $\times$ Height $\times$ Season	6			n.s.			n.s.			n.s.

Non-significant 3-way and 2-way interactions were eliminated from the final model.

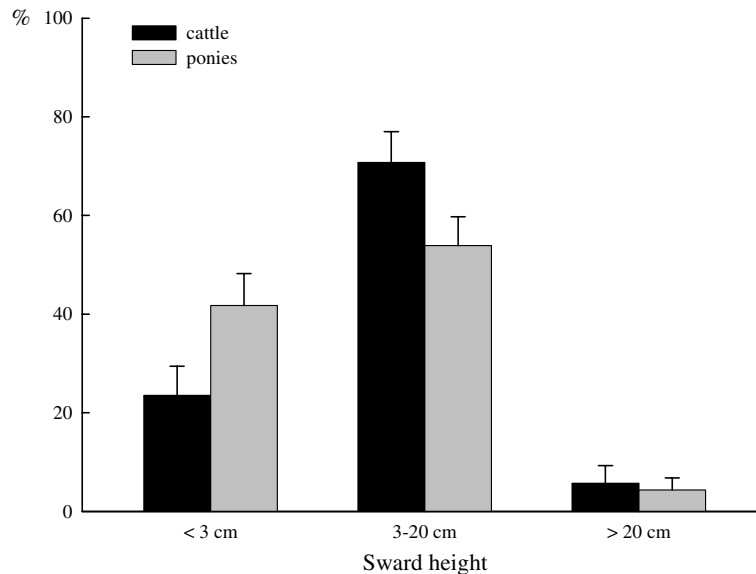


Fig. 3. Proportion of the grazing time, when foraging in grasslands, spent in the different sward heights.

Table 5

Plant species from which more than 500 bites were taken during the 30 sessions of 6-h periods for both cattle and ponies

Plant species	Class	% Bites
Highland cattle		
Mix of graminoids	G	79.31
<i>Carex arenaria</i> L.	G	2.83
<i>Juncus subnodulosus</i> Schrank	G	2.00
<i>Rubus caesius</i> L.	F	1.83
<i>Holcus lanatus</i> L.	G	1.60
<i>Claytonia perfoliata</i> Donn ex Willd.	F	1.53
<i>Urtica dioica</i> L.	F	1.51
<i>Salix repens</i> L.	W	1.32
<i>Rosa pimpinellifolia</i> L.	W	0.91
<i>Calamagrostis epigejos</i> (L.) Roth	G	0.89
Mix of forbs	F	0.73
<i>Carex riparia</i> Curt.	G	0.72
<i>Hippophae rhamnoides</i> L.	W	0.62
<i>Prunus spinosa</i> L.	W	0.62
<i>Clematis vitalba</i> L.	W	0.54
Shetland ponies		
Mix of graminoids	G	74.36
<i>Carex arenaria</i> L.	G	5.78
<i>Holcus lanatus</i> L.	G	3.94
<i>Claytonia perfoliata</i> Donn ex Willd.	F	3.82
<i>Scirpus setaceus</i> L.	G	3.22
<i>Carex riparia</i> Curt.	G	1.30
<i>Agrostis stolonifera</i> L.	G	1.17
<i>Calamagrostis epigejos</i> (L.) Roth	G	1.14
<i>Juncus subnodulosus</i> Schrank	G	1.14
Mix of forbs	F	0.66
<i>Rubus caesius</i> L.	F	0.49
<i>Poa trivialis</i> L.	G	0.48
<i>Stellaria media</i> (L.) Vill.	F	0.47
<i>Urtica dioica</i> L.	F	0.25

Class: G: graminoids; F: forbs; W: woody plants. 'mix of graminoids' and 'mix of forbs' was used to register a bite which contained several graminoid or herb species, difficult to identify on the species level, for example when the herbivores were grazing in short sward heights.

First, we considered the variation in the 'overall' diet composition, consumed over the total area. The proportion of bites was significantly different between Forage classes ($F_{2,160} = 480.44$; $P < 0.001$). In addition, the pattern is influenced by Species and Season as shown by the significant interactions Species $\times$ Class ($F_{2,158} = 15.42$; $P < 0.001$) and Season $\times$ Class ($F_{6,161} = 4.89$; $P < 0.001$). In all seasons the graminoids were the main component of both the cattle's and the ponies' diet (Table 6). The contribution of forbs and woody plants to the diet varied among seasons, for example in spring, both cattle and ponies incorporated a considerable proportion of forbs in their diet. Woody plants were only consumed by cattle.

Secondly, diet composition depended on the foraged habitat type or vegetation unit. In Table 6 diet composition of cattle and ponies when foraging in all distinguished habitat types and vegetation units is presented. It is not surprising that woody species were not present in the diet of the grazers when they were foraging in grassland. We investigated the diet composition of both species when they foraged in the grasslands with scrub invasion. In this vegetation unit there exists a potential to increase the proportion of woody plants in the diet. The factor Class ($F_{2,120} = 835.38$; $P < 0.001$) and the interaction Species $\times$ Class ($F_{2,120} = 6.61$; $P = 0.002$) had a significant effect on the proportion of bites per forage class. When foraging in grasslands with scrub invasion, the cattle increased the proportion of woody plants and forbs in their diet compared with their diet in grasslands, but graminoids remained by far the most important forage class of the diet. Ponies did not change their diet com-

Table 6

Diet composition of the cattle and ponies when foraging in the total area (level 1), the three habitat types (level 2) and the five vegetation units (level 3), averaged over the four seasons

Foraging level		Cattle			Ponies		
		%G	%F	%W	%G	%F	%W
1	Total area	87	8	5	92	8	0
2	Grassy habitat	95	2	3	95	5	0
	Scrub	73	6	21	96	4	0
	Woodland	59	27	14	72	28	0
3	Open vegetation and moss dunes	65	27	8	81	19	0
	Grasslands	99	1	0	97	3	0
	Grasslands with scrub invasion	92	3	5	97	3	0
	Rough grasslands	96	0	4	99	1	0
	Rough vegetation	94	1	5	93	4	3

%G: proportion of bites taken from graminoids. %F: proportion of bites taken from forbs. %W: proportion of bites taken from woody plants.

Table 7

Habitat use and Forage use overlap between cattle and ponies (Kulczynski's index)

	Summer	Autumn	Winter	Spring
Habitat use overlap				
Level 1	0.78	0.87	0.81	0.83
Level 2	0.70	0.96	0.72	0.67
Level 3	0.83	0.71	0.91	0.76
Forage use overlap				
Total area	0.93	0.92	0.94	0.98
Grassy habitat	0.95	0.98	0.96	0.92
Scrub	0.81	0.66	0.89	0.69
Woodland	0.71	0.63	0.64	0.84
Open vegetation	— ^a	0.98	0.80	0.71
Grasslands	0.97	0.99	0.96	0.97
Rough grasslands	0.90	0.98	— ^b	1.00
Grassland with shrub	0.94	0.94	0.86	0.96
Rough vegetation	0.96	0.96	0.91	0.99

Habitat use overlap was calculated at three levels. Level 1: Overlap in the use of the three habitat types: grassy habitat, scrub and woodland. Level 2: Overlap in the use of the five vegetation units within the grassy habitat: open vegetation, grasslands, rough grasslands, grassland with shrub invasion and rough vegetation. Level 3: Overlap in the use of the three sward heights within the grasslands: <3 cm, 3–20 cm and >20 cm. Forage use overlap was calculated within the total area, the three habitat types and the five vegetation units within the grassy habitat.

^a Both cattle and pony did not forage in open vegetation in summer.

^b Cattle did not forage in rough grassland in winter.

position in the grassland–scrub mixture compared to the diet in grasslands.

Finally, we examined how the diet composition differed between both species when they were foraging in scrub in autumn, the season in which both species foraged a lot in scrub. The proportion of bites was influenced by the factor Class ($F_{2,41.3} = 70.32$; $P < 0.001$) and by the interaction Species $\times$ Class ($F_{2, 41.3} = 28.79$; $P < 0.001$). In general, graminoids were still the main component of the diet, for the ponies (98.6%) as well as for the cattle (64.8%). However, there was a remarkable difference between the two species. The cattle increased the proportion of forbs (13.1%) and especially woody plants (22.1%) in their diet. By contrast, the po-

nies foraging in scrub in autumn only rarely consumed woody plants (0.3%) and forbs (1.1%).

3.4. Niche breadth and niche overlap

Over the whole year cattle and ponies had a similar habitat niche breadth (4.80 and 4.91, respectively). Ponies had highest habitat niche breadth in spring and lowest in summer (Su: 3.01; Au: 3.29; Wi: 3.57; Sp: 4.57). Cattle had highest habitat niche breadth in summer and lowest in winter and spring (Su: 5.35; Au: 3.57; Wi: 2.71; Sp: 2.84).

We found that the cumulative distance travelled over the 6-h observation period was similar for the two

species (cattle: 590 ± 50 m; ponies: 630 ± 31 m) and was not significantly different among seasons.

The high abundance of graminoids in the diets of both herbivore species is also reflected in the niche breadth index based on forage use. Both species had rather low forage niche breadth indices, with cattle having a bit higher niche breadth than ponies (1.40 and 1.19, respectively). Cattle and ponies had highest forage niche breadth in winter and spring, respectively, both had lowest forage niche breadth in autumn.

Table 7 presents the habitat use and forage use overlap indices. Seasonal variation in habitat overlap depended on the level of spatial organisation considered, but was overall high. The cattle and ponies had highest habitat overlap in autumn, both when choosing between grassy habitat, scrub and woodland and when choosing the vegetation units within the grassy habitat. Contrarily, in autumn they showed lowest habitat overlap within the grassland, when choosing between the different sward heights. Considering all the bites taken in the total area forage use overlap is very high. Also when grazing in the grassy habitat both cattle and ponies foraged the same forage classes. Calculating the forage use overlap in each vegetation unit within the grassy habitat gives again very high overlap values. A bit smaller values are found for the forage use overlap within scrub and within woodland.

4. Discussion

4.1. Grazing behaviour

Ponies spent a lot more time to foraging than cattle, which corresponds with the findings of previous studies (Arnold and Dudzinski, 1978; Arnold, 1984; Menard et al., 2002). During a 6-h period ponies spent, on average, 2 h more on grazing than did cattle and they did so in every season. Throughout the year the ponies in the Westhoek achieved high grazing times (70.7% of their time). These high grazing times are not extremes but are situated around the upper limit when compared with other studies. Jarrige and Martin-Rosset (1987) reported that feral horses spend 50–73% of their time on grazing during daylight. Przewalski horses in a nature reserve in the Mongolian steppes were only grazing an average of 49% of the daytime (van Dierendonck et al., 1996). Duncan (1985) concluded that feeding of Camargue horses generally occupies 50–70% of a whole day. Grazing times of the cattle in the Westhoek (38.4% of their time) are in the range reported in other studies. Cattle free ranging in the Camargue grazed for 36–48% of their time (Menard et al., 2002). Arnold and Dudzinski (1978) reported that cattle were grazing for 32–40% of their time.

During the summer both herbivores spent less time grazing, while in winter feeding time reached higher levels. Cattle increased grazing time in winter by 52% compared to summer and ponies increased grazing time by 14%. This increased grazing activity in winter is well known for horses (Duncan, 1983, 1985; van Dierendonck et al., 1996; Berger et al., 1999; Cosyns et al., 2001; Menard et al., 2002), and has also been reported for cattle (Arnold and Dudzinski, 1978; Pratt et al., 1986; Menard et al., 2002). However, other studies (van Wieren, 1996; Vulink, 2001) reported minimum grazing activities of cattle in mid-summer and mid-winter. Two contrasting mechanisms may play a role. When less forage is available intake rate is reduced and compensation may occur by an increased grazing time. Contrarily, the more fibrous food in winter can result in a faster rumen-fill effect and so in a decreased grazing time. Additionally, it has been suggested that cattle have a reduced metabolic rate in winter and that they are subject to an endogenous physiological rhythm resulting in a seasonal variation in voluntary food intake. Voluntary food intake would be lowest in winter (see van Wieren, 1996). The cattle in Westhoek had a very low bite rate in winter, which may be the result of the decreased forage availability. The increased daily grazing time may then be a compensation for the low bite rate.

With similar mean bite rates for both herbivore species (cattle: 29 bites/min; ponies: 31 bites/min) the ponies achieved a much greater number of bites over the 6-h period due to their higher grazing times. Averaged by season, bite rate and number of bites were highest in spring, when plant growth starts and provides the herbivores with high quality forage.

4.2. Habitat use

Throughout the year, cattle and ponies foraged in all the available habitat types, though their foraging activities were not distributed over the various habitats according to the availability of these habitats. Grassy habitat was preferred by both cattle and ponies, while scrub was avoided (according to the Jacobs' selectivity index (1974)). Within the grassy habitat, the grasslands and grasslands with scrub invasion were preferred, rough grasslands were only preferred by ponies, rough vegetation was not preferred nor avoided and moss dunes and open vegetation were avoided. In diverse ecosystems where habitat use of large herbivores has been studied, the same preference for grasslands is found (Camargue: Duncan, 1983; Menard et al., 2002; New Forest: Pratt et al., 1986; Putman et al., 1987; Rhum: Gordon, 1989a). In addition, habitat use was clearly influenced by seasonal characteristics. As expected, grasslands were less favoured in winter and grazing activity was then partly transferred to other habitat types. However, the ponies in the Westhoek, like the

New Forest ponies (Pratt et al., 1986), maintained high grazing times in grasslands during winter. In summer the scrub habitat was grazed only by cattle, but in autumn and winter cattle as well as ponies increased their foraging time in scrub. In spring both cattle and ponies foraged a lot in woodland, it was even a preferred habitat then. The lower plant productivity of the grasslands during the non-growing season is the most probable reason for the observed shift in habitat use (Gordon, 1989b; Gordon and Illius, 1989). In addition, some forbs such as *Claytonia perfoliata* (locally an important component of the scrub and woodland undergrowth) offer green biomass of high quality during winter and spring and 'attract' the grazers towards scrub and woodland.

Although grassy habitat was grazed intensively by both cattle and ponies, the Shetland ponies concentrated their grazing time more on the grass-dominated habitats than did the cattle. Throughout the year the cattle spent a greater proportion of their grazing time in scrub and woodland as compared to the ponies (cattle: 45%; ponies: 21%). In the Camargue study of Menard et al. (2002) there was no habitat type dominated by shrubs or trees, but the coarse grasslands with shrubs and the salt flats with woody plant species were grazed more by the cattle than by the horses.

Although cattle and ponies in the Westhoek had similar averaged bite rates, this is not true in all habitat types. Ponies maintained a more or less constant bite rate in the various vegetation types, unlike the cattle with a decreased bite rate in scrub, woodland and open vegetation. In the grasslands, rough grasslands and rough vegetation cattle grazed faster than ponies. Factors like searching time, handling time and mastication time determine the bite rate (Spallinger and Hobbs, 1992). For example, a decreased bite rate can be the result of an increased searching time, because of less avail-

able food items, or of an increased browsing activity. The latter might explain the decreased bite rate of cattle in scrub and woodland. In Fig. 4, we show the relationship between the cattle's bite rate in a habitat type/vegetation unit and the proportion of woody plant species in the cattle's diet consumed in that habitat type/vegetation unit. A considerable amount of the cattle's diet when foraging in scrub and woodland consisted of woody plants, which could explain the decreased bite rate in these habitats.

In the grasslands, intensively grazed by both herbivores, there was a differentiation in the sward heights used by the two ungulates. In the grasslands the ponies took 42% of their bites from very short swards and 54% from swards of 3–20 cm. In contrast, cattle took only 24% of their bites from short swards and 71% from swards of 3–20 cm. The values do not indicate any preference or avoidance as we have no data about the availability of the different sward heights. As expected the cattle grazed less in the short swards than the ponies, which was also concluded in the study of Menard et al. (2002). Contrary to the cattle in the New Forest (Putman, 1996) and on the Isle of Rhum (Gordon and Illius, 1989) the cattle in the Westhoek did not abandon the very short grasslands in winter, although the grasslands in general were grazed less by the cattle in winter. It should be noted though that very short sward grasslands in the study area are not concentrated in large patches as is the case in the New Forest and the Isle of Rhum sites but are in a small-scaled mosaic with the other sward heights. The smaller proportion of bites taken by cattle in the short swards is the result of the smaller proportion of grazing time spent on the short swards, and not of a lower bite rate. In contrast, cattle achieved a similar bite rate on short swards as ponies (41 and 39 bites/min, respectively). It is often suggested that bovids are morphologically constrained to graze on short swards because of the lack of the upper incisors (Illius and Gordon, 1987). However, in the Westhoek the cattle maintained a high bite rate on swards with a height of less than 3 cm. The high bite rate might be an indication that the cattle had no morphological problem to graze this sward height. Though, it is probable that the constraint may rise on swards from less than 2 or 1 cm. Furthermore, it is possible that when grazing the short swards the bite mass of cattle is much smaller than the bite mass of ponies due to mouth morphology. As a consequence cattle might be restricted in their effort to consume enough biomass on the short swards to fulfil their nutritional needs. Areas of the grasslands are maintained very short by the grazing activity of the ponies, which provide themselves in such a way of high quality vegetation where only the ponies are able to obtain enough biomass. In addition, when the herbivores grazed on swards of 3–20 cm, the ponies had a bite rate of 29 bites/min, while cattle reach the level of

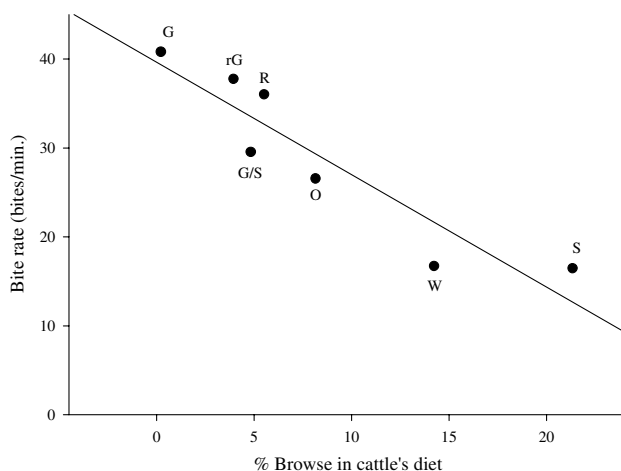


Fig. 4. Relation between the percent browse in the cattle's diet and the bite rate when foraging in the different habitat types. G: grasslands; rG: rough grasslands; R: rough vegetation; G/S: grasslands with scrub invasion; W: woodland; O: open vegetation and moss dunes; S: scrub.

39 bites/min. Thus, while short swards can be a constraint for cattle (too little biomass), higher swards might be a constraint for horses. Although the higher swards will provide forage of a lower quality, compared to the shorter swards (Van Soest, 1982; WallisDeVries and Daleboudt, 1994), these grassland patches of 3–20 cm height still provide forage of good quality. In addition, the herbivores are able to achieve enough ‘bulk’ food in a short time in the higher swards. Within the grassland the sward heights of more than 20 cm were rarely grazed by cattle or ponies. Patches of this height probably contain high levels of senescent plant material and the quality of grasses declines fast to low levels with advancing maturity (Cook, 1972). Studies of patch selection by cattle within grassland reported that cattle preferred short vegetative patches (<7–8 cm) even though they could have achieved greater intake rates on taller mature patches (WallisDeVries and Daleboudt, 1994; Ginane et al., 2003).

4.3. Diet composition

Horses are considered as true grazers that feed predominantly on grasses (Van Dyne et al., 1980; Putman et al., 1987; Duncan, 1992; Hoffmann et al., 2001; Co-syns et al., 2001; Vulink, 2001), which is confirmed in this study as well. Although the contribution of forbs and woody plants to the diet was higher for cattle than for ponies, the cattle in the Westhoek should also be considered as true grazers. There was a high dietary overlap throughout the year in our study, which is in line with other studies (Olsen and Hansen, 1977; Krysl et al., 1984; Vulink, 2001; Menard et al., 2002). Forbs are consumed considerably more in spring compared to the other seasons by both cattle and ponies, resulting in a slightly decreased importance of graminoids during that season. Browsing of woody plants occurred by cattle but not by ponies, with highest browsing intensity in summer which is rather surprising. Despite the higher proportion of woody plants in the cattle’s diet in summer, highest absolute number of bites from woody plants was taken in winter and autumn, because of the increased grazing time in winter and autumn compared to summer. In the preferred grasslands both herbivore species concentrated almost totally on graminoids, though in the grasslands with scrub invasion the cattle increased the proportion of woody plants in their diet. Overall, the cattle consumed a higher proportion of dicotyledons than the ponies, as we hypothesized since cattle are able to detoxify plant secondary compounds, commoner in dicotyledons than in monocotyledons.

4.4. Implications for conservation management

In the Westhoek grazing management has been implemented to maintain (or upgrade) the species-rich

grasslands and to avoid the further encroachment of the dense scrub layer which already covers almost half of the area. Conservation management concentrates on the prevention of the further expansion of dominant grasses and shrub species, such as *Calamagrostis epigejos*, *Arrhenatherum elatius*, *Holcus lanatus*, *Hippophae rhamnoides*, *Salix repens* and *Ligustrum vulgare*. The domesticated grazers are expected to act as selective ‘mowing machines’ and nature management hopes that the domestic grazers consume those species that management would like to be seen diminished. Horses need to consume more dry matter per kilogram bodyweight than cattle to fulfil their nutritional requirements (Menard et al., 2002). In that sense, a pony of a given weight is a better ‘mowing machine’ than a cow of similar weight, because it ‘cuts down’ more vegetation. Using the data of Menard et al. (2002) one Highland cow of 481 kg consumes a similar quantity of dry matter as does one Shetland pony of 205 kg (4.7–12.2 and 5.5–11.6 kg dry matter per day, respectively). Differences in removal of vegetation biomass will depend on the differences in diet composition. The ponies consume predominantly graminoids and they are more able to graze the vegetation close to the ground, than the cattle. Throughout the year, ponies spent 79% of their grazing time in the grass-dominated vegetation units and are thus very suitable to maintain grassland habitats. However, the ponies do not browse and consequently have no impact on the scrub invasion into the grasslands. Cattle perform browsing activity, varying with season and foraged vegetation unit. In contrast to ponies, while foraging in the grasslands with scrub invasion the cattle did not only consume graminoids, but also browsed on shrubs (e.g. *Salix repens*, *Hippophae rhamnoides* and *Ligustrum vulgare*). In addition, the cattle grazed less in the grassy habitats than the ponies, but spent up to 26% of their grazing time in scrub. Thus, the cattle have a potential impact on scrub vegetation, not only by the direct consumption, but also by opening the closed scrub layer due to their movements. As a consequence of their large body size and their wide horns the cattle open the scrub layer. It has been observed that individual shrubs were partly damaged when the cattle moved through a scrub layer. The cattle’s use of scrub opened up this very dense vegetation and subsequently the ponies made use of these gaps to forage on graminoids in the scrub. We hypothesize that if the ponies would be the only herbivores in the reserve, foraging in scrub would occur far less frequently, because the ponies avoid moving through a densely closed vegetation structure. Foraging in scrub vegetation is likely to make this vegetation type less vital and will create gaps, important for the establishment of other plant species.

Another implication for nature management is that the cattle foraged more in the entire reserve than the

ponies. Our map with locations shows that habitat use on the landscape level (Senft et al., 1987) is broader for cattle than for ponies. One central grass-dominated entity in the Westhoek counted 27.8% of the cattle locations and 54.3% of the pony locations. Thus, the impact of grazing by ponies is more concentrated, while other areas receive consequently no or less grazing impact by the ponies. Similarly, Vulink (2001) found that Konik horses concentrated on the short grasslands for most of the year and cattle foraged more over the entire area (Oostvaardersplassen in the Netherlands).

As a management tool, a combination of cattle and ponies seems to be adequate for the objectives of the nature management (see also Loucougaray et al., 2004). However, with only four cattle grazing in the reserve, a further increase of invasive shrub species will probably not be halted on the long run.

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