Foraging behaviour and habitat use of large herbivores in a coastal dune landscape.

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Foraging behaviour and habitat use of large herbivores in a coastal dune landscape.

Foerageergedrag en habitatgebruik van grote herbivoren in een kustduinlandschap.

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1 GENERAL INTRODUCTION

DONKEYS IN A MOSS DUNE , HOUTSAEGERDUINEN (FOTO: INDRA LAMOOT)

Foraging behaviour and habitat use of large herbivores

Free-living animals constantly make foraging decisions in order to survive, to grow and to bear off-spring with good survival chances, in short, to contribute to fitness. Discrepancies between qualitative and quantitative food *demands* and the characteristics of the *available* food are the main reason for the necessity of these foraging decisions. These decisions should lead to an efficient foraging behaviour. Habitat use is the 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 & Gordon, 1993). Food resources in the natural landscape are distributed in a mosaic of patches of variable size and shape with a fluctuating quantity and quality of food (WallisDeVries, 1994). The abundance of consumable material in the vegetation surrounding a herbivore varies enormously with regard to the nutritive value to the herbivore. The herbivore has to select the real food from the apparent buffet in order to obtain a balanced diet. An efficient foraging behaviour contributes to the consumption of sufficient food, both in a quantitative and qualitative way. In trying to understand what determines a consumer's actual diet, ecologists have increasingly turned to optimal foraging theory (reviewed by Stephens & Krebs, 1986). One assumption of the theory is that animals forage to maximize nutritional gain per unit cost. The most widely used version of the model concerns the maximization of energy intake as currency and is thought to be more appropriate for carnivores than herbivores (Provenza & Balph, 1990). For many consumers (particularly herbivores and omnivores) the efficient gathering of energy may be less critical than some other dietary constituent (e.g. nitrogen), or it may be of prime importance for the forager to consume a mixed and balanced diet. In such cases, the value of existing optimal foraging theory is limited (Begon et al., 1996). The true currency that the herbivore is optimising remains to be identified (Rook et al. 2004). There is much debate about the value of optimal foraging theory for predicting the herbivore's foraging behaviour (Belovsky, 1990; Provenza & Balph, 1990; Fortin et al., 2003). However, optimal foraging theory has been applied to large herbivores with some success. Classical models of ungulate foraging are based on the optimal foraging theory: e.g. the linear programming model (Belovsky, 1978), the clever ungulate model

(Owen-Smith & Novellie, 1982). Optimal foraging theory has been valuable in stimulating research on foraging behaviour and providing a quantitative focus for that research (Provenza & Balph, 1990).

Foraging models imply a large degree of simplicity. This is mostly in contrast with the real world of a large herbivore. We here try to identify the main aspects playing a role in the foraging behaviour and habitat use of free-ranging ungulates, living in a spatially and temporally heterogeneous environment. The relation between the animal and its food supply is determined by the characteristics of the environment on the one hand and the characteristics of the herbivore on the other.

The heterogeneous environment

The free-ranging horses and cattle, subject of this study, are all foraging in a heterogeneous environment, heterogeneous at different spatio-temporal scales. It is evident that the foraging animal has to make more foraging decisions in a heterogeneous than in a homogeneous environment. Senft et al. (1987) presented the ecological hierarchy encountered by large herbivores while foraging: regional scale, landscape scale, plant community scale and patch level. In our study the animals are restricted in their movement patterns because they live in fenced, relatively small areas (all < 100 ha), as such presumably smaller than the natural home range. As a consequence, the herbivores are not confronted with decision-making at the highest ecological level, i.e. at the regional scale. The first level applicable in our study areas is the landscape level. At this level the animals select among the different plant communities. Within a plant community there are various patches differing in nutrient quality and quantity. Thus, the animal has to decide in which patch to graze, i.e. decision at the level of the plant community. At the level of the patch the herbivore chooses a feeding station within the patch, e.g. a certain plant species, plant individual, plant part. Decisions at a higher level influence decisions at a lower level. Senft et al. (1987) calculated that large herbivores cross plant-community boundaries as many as 50 times/day, implying a decision frequency at the landscape level in the order of 10^4/year. It is clear that this decision frequency depends on the spatial configuration of the plant communities. If preferred plant communities are present as large connected patches, then decision frequency at the landscape scale will be lower than if the preferred plant communities are distributed patchily over the area separated by unfavourable plant communities. At the regional and landscape scale non-forage features, e.g. shelter or location of water, interfere with forage characteristics in the decision making. The decisions at the lower levels are primarily made in function of forage characteristics. It is widely accepted that forage abundance and forage quality play a major role in foraging behaviour. Forage quality is related to the availability of energy, proteins and minerals as well as to the absence of plant toxins. Plant species, as well as individual plants within species and plant parts vary in these features. Furthermore, the nutritive value of a plant changes during its (seasonal) life cycle (Owen-Smith, 1982). Other aspects of the vegetation than forage quality and quantity may influence patch selection as well, e.g. sward height, stem:leaf ratio (WallisDeVries & Daleboudt, 1994; Bergman et al., 2000; Ginane et al., 2003). Morphological plant defences, like thorns and spines, can hinder intake or decrease ingestion rate (Cooper & Owen-Smith, 1986), and therefore can play a role in the selection of plant species. These morphological defences are especially present in species with a high nutritive value (Van Wieren, 1987). Additional to the spatial heterogeneity, temporal variation in the environment influences the foraging herbivore. Nutritive quality and the availability of most plant species and thus plant communities are highly variable among seasons, with a decreased quality and availability in the non-growing seasons (i.e. autumn and winter in temperate regions) (Bokdam & WallisDeVries, 1992; Duncan, 1992). The decisions at all levels are assumed to be strongly affected by this seasonal variation in food. Seasonal variation not related to forage characteristics can also play a role, e.g. in dry seasons the animals may prefer to graze in the proximity of water. Additionally, the large herbivores are also confronted with non-seasonal temporal variation of the environment. For example a spot of high nutritive value may be reduced in its quality because other herbivores were foraging this spot recently.

The large herbivores

The nutritional requirements of large herbivores depend on a large number of intrinsic, as well as extrinsic factors (e.g. weather conditions). Different animal species, different animal breeds as well as different individual animals may show considerable variation in their nutritional demands. The variation at the level of the animal species can be attributed to several intrinsic factors, including digestive system, metabolic rate and body size. Likewise, these factors may be on the basis of differences in nutritional demands between animal breeds. The digestive system is in general similar within a species, but subtle differences in digestive efficiency between breeds may result in other needs. Body size, age, reproductive state, health condition, background can vary widely among individuals of the same breed, resulting in different demands.

Cattle vs. equids, ruminant vs. non-ruminant

Three major groups of herbivores are foraging in the study areas: herbivorous insects, small mammals (rabbits, mice, etc.) and the introduced ungulates, our study subjects. Depending on the used discriminative criteria ungulates are divided into several groups. Ungulates comprise three taxonomic orders: the Proboscidae, the Perissodactyla and the Artiodactyla. Elephants and related extinct mammoths and mastodons form the Proboscidae. The Perissodactyla are the odd-toed ungulates (tapirs, rhinoceroses and equids). The Artiodactyla are the even-toed ungulates (pigs, hippopotamus, camels, giraffes, cattle, deer, sheep and goats) (Dorit et al., 1991). According to their digestive system ungulates are divided into ruminants and non-ruminants. Ruminants (or foregut fermenters) developed a complex fermentation system with multiple chambers in the stomach and a major role for cellulose-digesting microorganisms. The herbivores need to ruminate the partially digested, regurgitated forage. Non-ruminants (or hindgut fermenters) do not have a multiple stomach system and fermentation takes place in the ceacum and colon. Most even-toed ungulates are ruminants with the exception of pigs and hippopotamus (about the camel's fermentation system there still exists uncertainty (Van Soest, 1994)). Pigs are not strictly herbivores and have an adapted digestive system.

Hippopotamus are non-ruminant foregut-fermenting herbivores (Clauss et al., 2003a). Elephants and the odd-toed ungulates are non-ruminants. Hofmann (1989) classified the ruminants into three feeding types: concentrate selectors, intermediate feeders and grass and roughage feeders. Concentrate selectors (also called 'browsers'), e.g. roe deer, have a digestive system that is far less suited to optimize plant fibre digestion and search for a high quality diet. Grass and roughage feeders (also called 'bulk feeders' or 'large grazers') are able to digest plant items with a high cell wall content and forage large amounts of fibrous food, i.e. grasses and roughage. Domestic cattle and sheep belong to this group. The intermediate feeders (also called 'mixed feeders') are in between the two former types and choose a mixed diet. Red deer and domestic goat are examples of intermediate feeders of the temperate region. Hofmann's classification is based on the relationship between the predominant type of food and observed morphological and postulated physiological characteristics of the digestive system (Hofmann, 1989). The classification is widely accepted, though has also been questioned especially in terms of the morphophysiological explanations (Pérez-Barberia & Gordon, 1999a, 1999b; Clauss et al., 2003b). The underlying mechanisms are not unravelled yet, but Hofmann's classification is certainly useful to divide ruminants in groups according to their predominant type of food and, related to this, their foraging behaviour. Based on their diet we could assign equids, which are non-ruminants, to the group of grass and roughage feeders in Hofmann's classification.

The present study deals with the foraging behaviour of equids (Equidae) and cattle (Bovidae). The domestic donkey, a breed belonging to the species *Equus asinus*, and the Shetland pony, Haflinger horse and Konik horse, all breeds belonging to the species *Equus caballus*, are the studied equids. The domestic cattle breed of *Bos taurus* under study is Scottish Highland.

The nutrients, 'captured' in the consumed food items, become available to the herbivore through digestion and nutrient absorption. To digest cellulose and hemicelluloses, the fibrous fractions of cell wall material, cellulase is needed, an enzyme which is not secreted by mammals. Therefore, forage feeders must either select very high quality diets or rely on a symbiotic relationship with cellulose-digesting microorganisms, which house in enlarged sections of their gastro-intestinal tracts. Ruminants and non-ruminants have developed different solutions to cope with cell wall material (Rittenhouse, 1986).

In ruminants (polygastric animals) cellulose-digesting microorganisms are confined to the rumen and reticulum, two of the four chambers of the stomach. The partly digested forage is regurgitated and the animal chews it again, i.e. rumination, resulting in a further mechanical breakdown of the plant material. The microorganisms have a twofold function since they are digested in a subsequent part of the stomach and become a source of amino acids and vitamins.

Microorganisms also play a role in the equid's digestive system. Fermentation of cellulose by the microorganisms takes place after the food has passed the stomach ("hindgut fermenters"), because the microorganisms are present in the caecum and colon. There they can not be digested and thus amino acids and vitamins present in the microorganisms are lost with the faeces.

What are the advantages and disadvantages of both systems? The major advantage of the ruminant system compared to the non-ruminant system is the greater efficiency of extraction of nutrients from the cell wall. At the other hand, non-ruminants are able to utilize the soluble components of the cell more efficiently than ruminants, since nutrients are absorbed directly without losses to fermentation. When available food is of low quality, the intake rate of ruminants is constraint by the rate of the fermentation process, which will be more slowly for a cellulose rich (low quality) diet, while non-ruminants are restricted only in the availability of forage and grazing time (Rittenhouse, 1986). Many authors have focused on the question about which system is the best, especially in terms to explain why cattle are more species rich and more abundant than equids. The 'nutritional model' (Bell, 1971; Janis, 1976; Foose, 1982) describes the effect of forage fibre on nutrient extraction rates in ruminants and non-ruminants. The authors state that on medium quality forages ruminants are assumed to extract more nutrients per day than hindgut fermenters, while on very high quality as well as on low quality forages hindgut fermenters should achieve higher rates of nutrient extraction than do ruminants. Duncan et al. (1990)

tested this model and concluded that equids retained the forages in their digestive tract for a shorter period of time and digested the forages less completely than cattle. However, the equids achieved higher intakes of forages. As a result the extraction for nutrients was higher in equids than in cattle, both on low quality food as on medium quality food. Their results could only partly support the nutritional model of Bell (1971), Janis (1976) and Foose (1982). Illius & 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, since ruminants require 20% less food to obtain the same energy yield, compared to equids of similar body size. They suggest that the predominance of ruminant species in the intermediate body weight range has arisen through superiority under conditions of resource limitation rather than their superior ability to extract nutrients from abundant food. Duncan et al. (1990) have put forward that the evolutionary success of the ruminants may be built on the ability of the rumen flora to detoxify plant secondary compounds (Prins, 1987), which is not known for equids. Secondary compounds can restrain digestion (Joenje, 1987). It is recognised that secondary plant compounds play an important role in the interaction between herbivores and their forage.

Variation among equids and among individuals

Donkeys, Haflinger horses, Konik horses and Shetland ponies are all hindgut fermenters with a similar digestive system. Although little information is available, some studies have reported on remarkable physiological differences between the donkey and other equids. In particular, several studies reported on the donkeys' capacity to deal with dehydration (Izraely et al., 1994) and with their increased digestive efficiency (Izraely et al., 1989; Cuddeford et al., 1995; Pearson et al., 2001). Izraely et al. (1989) found that the digestive efficiency of donkeys is as high as that of Bedouin goats, with the latter being more efficient than non-desert ruminants. The capacity of donkeys to digest plant cell wall constituents is lower than that of Bedouin goats and other ruminants but higher than that of ponies or horses. The donkey reaches the same efficiency as the Bedouin goat as a result of its higher intake rate and higher efficiency to absorb soluble cell content components. Cuddeford et al. (1995) compared the digestive efficiency among Thoroughbreds, Highland ponies, Shetland ponies and donkeys. Donkeys retained food longer in the digestive tract and digested fibre more efficiently than did the other equids. In that sense, donkeys were more 'ruminant-like'. This was confirmed by Pearson et al. (2001): compared to ponies, donkeys had longer retention times and a higher digestibility of dry matter, energy, crude protein and fibre fractions. Ponies compensated for their smaller digestive efficiency by consuming more dry matter per day compared to the donkeys. Beside these differences in digestive abilities, different equid species and breeds may differ in metabolic rate. Since voluntary food consumption is related to metabolic rate (Kleiber, 1961; Webster, 1985) and donkeys consume less dry matter per unit metabolic body weight than ponies (Pearson et al., 2001), we may assume that donkeys have a lower metabolic rate compared to ponies. Hence, donkeys probably have lower maintenance requirements as well. These differences in requirements and digestive abilities between equid species can lead to differences in their foraging behaviour in a free-ranging situation.

To our knowledge no reports exist on the possible variation in digestive efficiency among Haflinger horses, Konik horses and Shetland ponies (three breeds of *Equus caballus*), nor on variation in aspects of their behaviour. The studied equid groups differ in body size (Haflinger > Konik >> Shetland pony > Donkey) and this factor may also result in possible differences in foraging behaviour. In absolute terms, larger animals have higher nutritional demands than smaller animals (e.g. a horse of 200 kg needs 7.4 Mcal DE/day, a horse of 800 kg needs 22.9 Mcal DE/day for maintenance (NRC, 1989)). However, smaller animals need more energy per unit body weight than larger animals, since energy requirements scale with body mass to the power of 0.75, while gut capacity is isometric to body mass (Demment & Van Soest, 1985; Illius & Gordon, 1987), as illustrated also by the example above (a horse of 200 kg needs 37.0 cal DE/kg/day, a horse of 800 kg needs 28.6 cal DE/kg/day). Larger animals are able to use forage of lower quality than smaller animals, because the former can eat more and retain the cell wall fraction of food longer in their larger guts (Demment & Van Soest, 1985). Above that, large herbivores have larger mouth parts and are therefore unable to forage with a high degree of selectivity compared to

smaller herbivores (Illius & Gordon, 1990). Recent studies concluded that grazing time is negatively related to body mass in temperate ruminants (Mysterud, 1998; Pérez-Barberia & Gordon, 1999b); this has not been studied so far in the case of hindgut fermenters.
The effect of breed differences on foraging behaviour has only rarely been studied, and this only for cattle, sheep and goats (WallisDeVries, 1993; Dziba et al. 2003; see also Rook et al., 2004).

One of the main factors influencing the nutritional demands of individual animals is the reproductive state of these animals. Reproduction and mainly lactation is highly demanding for mammalian herbivores.
Concerning horses, it is generally accepted that the production of milk poses high nutritional demands on the lactating mares, especially during the first 3 months of the lactation period, when the amount of digestible energy and crude protein in the diet surpass the demands for maintenance with 86% and 132%, respectively. Also the demands for minerals increase strongly during lactation (NRC, 1989). As lactation progresses the demands decrease but stay higher than the maintenance requirements. Lactating females have to adjust their foraging behaviour to meet the increased nutrient requirements (NRC, 1989; Vulink, 2001).

Mechanisms to gain information of the environment

In a natural environment, a herbivore is surrounded by vegetation with a large variation in nutritive value in space and time. Nonetheless, the animal seems to be able to compose a diet, meeting its requirements. Otherwise it would not be able to survive in that environment. Although ecologists, ethologists and physiologists have tackled to some extent the question which mechanisms the herbivore can rely on to make the right foraging decisions, the question remains largely unsolved. The main problem for the herbivore is how to gain and process information about its foraging choices (Illius & Gordon, 1990). Herbivores must perceive differences among patches, plants and plant parts in order to be able to discriminate and select among alternatives (Bailey et al. 1996). Although it has been suggested that herbivores can directly sense nutrients and toxins in food, this is not widely accepted. Instead, there is increasing evidence that the sensory perceptions (sight, smell, taste, tactile) of the food enables the herbivore to make the relation with the nutritional and toxicological properties of the food through the process of association, with a major role for post-ingestive feedback (Provenza & Balph, 1990; Provenza, 1995). Perceptual events that cause malaise will establish a food aversion. Positive feedback, e.g. satiety, will establish food preferences. Some toxins may be readily sensed through taste or odour (Provenza et al., 1990). Next to post-ingestive feedback, there may exist also pre-ingestive feedback: in uterus and mother's milk. Young animals will most likely have been conditioned to prefer and avoid specific flavours that occur in foods before they have taken their first bite of solid food (Provenza & Balph, 1990). Association implies learning by consequences and memory. Young ruminants can remember specific foods that provided either aversive or positive consequences for at least 1 to 3 years. They also recognize and sample novel foods cautiously (see Provenza & Balph, 1990). Sampling is enormously important to large herbivores in order to utilize the resources of their environment as much as possible. They even have to sample familiar food items in familiar environments, because their nutrient content and toxicity change frequently (Provenza & Balph, 1990). How does a large herbivore deal with the information acquired at a higher ecological level than the level of the plant species, individual plants and plant parts? Large herbivores have to learn about the locations of resources in the environment (Provenza & Balph, 1990; Bailey et al. 1996). Cattle are known to use spatial memory, which is formed by two elements, i.e. reference and working memory. The reference memory is the map-like representation of the foraging environment. Working memory is essential to avoid that recently foraged patches are visited too soon again (Laca, 1998; Bailey et al. 1996; Bailey & Sims, 1998; Bailey et al. 2000). Visual cues seem crucial in the 'map building'. A certain level of heterogeneity is necessary in forming the spatial memory, though very complex spatial arrangements contain too much information to contribute positively to the memory building.

To summarize, it is common knowledge that large herbivores do not forage at random but take many foraging decisions at different ecological scales. Natural landscapes are mostly very heterogeneous in space and time. The more heterogeneous the environment, the more foraging decisions have to be made and the more complex the expressed foraging behaviour will be. As discussed above only some questions of the underlying mechanisms have been solved, mostly by means of experiments in simple artificial environments where the animals are confronted with only a few food alternatives. Far less information is available from spatially heterogeneous systems. The problem is to scale up simple experiments to complex landscapes or to explain observations from complex landscapes in terms of general mechanisms.

Habitat use as the expression of the foraging decisions

The habitat use of both horses and cattle have been more or less intensively studied in several semi-natural landscapes in the temperate region. Some well-known reports on habitat use are from the Camargue, a Mediterranean river delta in Southern France (e.g. Duncan, 1992; Menard et al. 2002), the New Forest in England, a large area (20000 ha) of deciduous woodland, heathland, bog and grasslands (e.g. Pratt et al., 1986; Putman, 1986; Putman et al., 1987) and the Isle of Rhum, Scotland (966 ha), with grasslands, heathland, bogs and littoral areas (e.g. Gordon, 1989a, 1989b, 1989c). In general terms, literature states that both cattle and horses preferentially select grassland communities, though they show seasonality in their habitat use with an increased use of less preferred communities in autumn and winter. High biomass of live graminoids and forbs was the main determinant of vegetation community selection on the Isle of Rhum, for both ponies and cattle (Gordon, 1989c). Van Dyne et al. (1980) reviewed the diet of large herbivores and found that the cattle's diet consisted for 72% of graminoids (N=121), the horses' diet consisted for 69% of graminoids (N=8). Despite these general similarities in foraging behaviour of cattle and horses, most comparative studies conclude that these two herbivore species differ in at least some aspects of their grazing behaviour when sharing the same living area (Pratt et al., 1986; Gordon, 1989b; Menard et al., 2002).

Until now, we have discussed habitat use in terms of the grazing behaviour. Above that we also want to discuss the habitat use for eliminative behaviour. It is widely accepted that cattle and horses perform a different pattern of eliminative behaviour, though both avoid eating in the vicinity of their faeces. Cattle in pastures drop their dung randomly over the entire area (Marsh & Campling, 1970, cit. in Edwards & Hollis, 1982), though there may be local concentrations of faeces near fences, gates and in areas where the animals group together at night. Horses grazing in pastures concentrate their faeces in latrine areas where they do not graze (Archer, 1972; Archer, 1973; Ödberg & Francis-Smith, 1976). Little information is known about these fouling patterns in more heterogeneous areas. Studies on the habitat use of free-ranging herbivores rarely discuss the eliminative behaviour. Tyler (1972) reported that there was no evidence that the ponies in the New Forest grazed and defecated in separate areas. Moehlman (1998a) stated that, in contrast with donkey stallions, female donkeys of all ages showed little interest in dung and simply defecated where they stood. In contrast, Edwards & Hollis (1982) found that the ponies foraging an area of grasslands in the New Forest established latrine areas, where they avoided grazing.

Habitat use and nature conservation

In Western Europe grazing management is increasingly being used as a tool for nature management in semi-natural landscapes. Since decades large domesticated herbivores, i.e. horses, cattle and sheep, have been introduced to maintain or restore biodiversity of heathland, grasslands, wetlands and coastal dunes (WallisDeVries et al., 1998). Large herbivores directly influence productivity, structure and diversity of plant communities (e.g. Vallentine, 1990; Archer & Smeins, 1991; Duncan, 1992; Bakker, 1998), mainly through their selective grazing, but also through trampling, rolling and eliminative behaviour. Tissue removal, litter reduction, modified light profiles, differentiated nutrient return through dung and urine, endozoochoric and epizoochoric dispersal of diaspores, are only a selection of the processes at the level of the individual plant. These processes may change competitive relations between plant species and consequently influence the composition of plant communities (McNaughton 1968). It is generally believed that herbivores enhance plant diversity by their direct consumption of competitively dominant species and providing better conditions for less-competitive plant species (Harper, 1977; Milchunas & Lauenroth, 1993).

However, detailed studies on the effects of herbivores on biodiversity have reported positive, weak as well as negative effects (Jefferies et al., 1994; Olff & Ritchie, 1998; Piek, 1998).

A major explanation for the high biodiversity of some areas in Western Europe with a long history of grazing management appears to be the differential herbivore pressure on various parts of a grazed area (WallisDeVries, 1995). The herbivores' differentiated habitat use influences strongly the outcome of the grazing management. Some parts will experience an 'intensive management', while in other parts there will be 'no management' at all. This pattern may be even more apparent in spatially and temporally heterogeneous landscapes. Nature management wants to know and understand the impact of the grazers on the grazed area. However, vegetation development under grazing occurs usually rather slow, especially at the higher ecological scales. For example, certain rare, but preferred plant species can disappear quite fast, but changes at the level of the plant community occur over a longer time period. Studies of the foraging behaviour and in particular the habitat use of the large herbivores contribute to gain a faster insight into the ongoing processes. As a consequence, the grazing management can be adjusted long before the impact on the vegetation would be visible.

Aim of the study

Different species and breeds of large ungulates have been introduced into several dune reserves along the Belgian coast as a management measure. The nature conservation expectations of this grazing management are high. However, management results and the predictability of them still carry a high level of uncertainty since little is known about the possible impact of the herbivores on such a relatively low-productive, heterogeneous ecosystem. This research does not aim to evaluate the grazing management in the first place, but aims to gain better insights into the (foraging) behaviour and the habitat use of the large herbivores in such a low-productive environment, with a considerable amount of spatial and temporal heterogeneity. We focus on different herbivore species and breeds, since we expect differences in their foraging behaviour and habitat use, due to their morphological and physiological differences. In the end, the results of the study are expected to contribute directly to the understanding of the herbivore impact.

The central hypothesis is that foraging behaviour reflects the nutritional ecology of the herbivores and provides a mean to gain insight in the mechanisms determining herbivore impact at the landscape scale.

Departing from the above mentioned characteristics of different ungulate species and breeds, we formulate the following hypotheses:

- Cattle and equids, living year round in low-productive areas where preferred grasslands (with good-quality grasses) cover only smaller parts of the area, are expected to perform a broader habitat use to meet their requirements. We hypothesize that the cattle and equids will also forage in vegetation types, which are normally less preferred for grazing by large herbivores, like scrub and woodland (Chapter 2.1 – 2.2 – 2.3).
- We hypothesize that large herbivores will adjust their foraging behaviour to seasonal changes in forage availability and quality, with an increased foraging activity in the less preferred vegetation units during autumn and winter (Chapter 2.1 – 2.2 – 2.3).
- Since cattle and ponies differ in many morphological aspects (e.g. Highland cattle being much heavier than Shetland ponies) and physiological aspects (e.g. cattle being ruminants and ponies being hindgut fermenters) we hypothesize that both species will differ in at least some aspects of their foraging behaviour and habitat use. We expect that niche differentiation will occur: either they will forage in different habitat types, or when foraging in the same habitats they will select niches with a different species composition and/or sward height. The niche differentiation is even more expected since both species are foraging together in a nutrient poor system with a high animal biomass density (Chapter 2.2.).
- Because lactating animals have higher nutritional demands than non-lactating animals we expect that lactating equid mares will perform an adjusted foraging behaviour compared to non-lactating mares. We predict that lactating animals would achieve a greater energy intake by grazing longer and/or biting faster, and hence take more bites than non-lactating mares (Chapter 3).
- It is known that horses grazing in pastures establish latrine areas

where they do not graze, but there exists much less certainty about the fouling patterns of equids grazing in large heterogeneous areas, with contrasting reports on this matter in literature. We hypothesize that equids, free-ranging in a relatively large heterogeneous environment, eliminate where they graze, in contrast to equids grazing in pastures (Chapter 4).

- We further expect that different equid species and breeds will show differences in at least some aspects of their foraging behaviour and habitat use, since they show important morphological (e.g. body size) and physiological differences (e.g. digestion efficiency). We therefore hypothesize that grazing time, biomass removal, browsing activity, vegetation selection, etc. will vary among equid groups, especially when comparing the donkey (*Equus asinus*) with horse breeds (*Equus caballus*).

Study areas

The research for this PhD was conducted in four study areas, situated in three nature reserves: ‘Westhoek’, ‘Houtsaegerduinen’ and ‘Ghyvelde’. The first two are located in the coastal dunes of Belgium, near the French border. The latter is an old dune area in France close to the northern French coastline and bordering an equally old dune ridge in Belgium (Figure 1.1). Climate in the coastal region is cool temperate with mild winters and mild summers. Mean annual temperature is 9.8 °C. In summer, autumn, winter and spring mean temperature is 15.9 °C, 10.8 °C, 3.9 °C and 8.7 °C, respectively; mean monthly precipitation per season is 60.7 mm, 74.8 mm, 56.5 mm and 48.5 mm, respectively (averaged over the period 1963-2002; Meteo WVL vzw).

All these reserves are relatively nutrient poor systems with a spatially heterogeneous vegetation pattern (see Maps A.1-4, Appendix). Biomass data (Cosyns, unpubl.) indicate relatively low levels of seasonal standing crop of the grassland types in the dune reserves compared to annual yield data of agricultural grasslands under different fertilizing levels (Table 1.1.; Table A.1-A.4, Appendix). Unfortunately, good figures on food quantity in the study areas are missing. Annual yield data are not available, while these would strengthen our assumption that the dune areas provide low forage quantity. More information is provided for forage quality. Crude protein content (as a measure for nutritive quality (France et al., 1999)) of the main graminoids

and herbs of the dune system (Cosyns, unpubl.) reach lower levels than those reported of graminoids and herbs typical for agricultural grasslands in the temperate regions (Table 1.2; Table A.5, Appendix).
Domesticated grazers were released for nature management reasons. They are free-ranging in the entire reserve (Ghyvelde and Houtsaegerduinen) or in parts of it (Westhoek). The herbivores remain in the area year round. During the research period, they received no additional food. Herd size and composition are controlled to avoid inbreeding and overgrazing.

Westhoek-North

The Westhoek 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-North' is a fenced area of 54 ha in the north of the Westhoek reserve, which is grazed by a herd of Konik horses and a small group of Highland cattle. The grazed area encompasses a relatively young dune slack zone, parts of the fore dune ridge and parts of the central large mobile dune. Scrubs of *Hippophae rhamnoides, Ligustrum vulgare* and to some lesser extent *Salix repens* occupy the largest part of the area. Before the start of the grazing project 12% of the original 79% scrub layer was cut down and removed, resulting in an area of ruderal vegetation composed of a low, grass-dominated layer (main species are *Holcus lanatus* and *Calamagrostis epigejos* and patches of tall herbs *Eupatorium cannabinum, Lythrum salicaria* and *Cirsium arvense*). The remaining area is covered by species-poor grassland, dominated by *Calamagrostis epigejos* or *C. canescens*, species-rich dune grassland with *Poa pratensis*, *Avenula pubescens, Veronica chamaedrys, Galium veru,* by young dune slack vegetation and moss dominated dune vegetation.
Grazing by Konik horses in Westhoek-North started in 1998 with two mares and two stallions. During the observation period (August 1998 – March 1999) the herd was enlarged with one foal (Table A.6, Appendix).

Westhoek-South

'Westhoek-South' (ca. 60 ha), a fenced area in the south of the Westhoek is grazed by a herd of Shetland ponies and a small group of Highland cattle. The area encompasses a dune slack zone and an inner dune ridge. Two thirds of this area is covered by more or less closed scrub vegetation: main shrub species are *Hippophae rhamnoides, Ligustrum vulgare, Crataegus monogyna* and *Prunus spinosa*; tree species are several Poplar species (*Populus x canadensis*, *P. tremula*, *P. canescens), Ulmus minor* and *Alnus glutinosa*. The other third of the fenced area is occupied by grasslands and herbaceous vegetations: species-rich dune grassland with *Poa pratensis*, *Avenula pubescens, Veronica chamaedrys* and *Galium verum*; tall herb vegetation with *Cirsium arvense, Eupatorium cannabinum, Lysimachia vulgaris, Lythrum salicaria* or *Iris pseudacorus*; patches of species-poor grassland enclosed by scrub, dominated by *Calamagrostis epigejos*; moss-dominated vegetation (*Tortula ruralis* ssp. *ruraliformis, Hypnum cupressiforme* var. *lacunosum* and *Brachythecium albicans* are dominants) and some marram dune (*Ammophila arenaria*) vegetation.

Eight Shetland ponies and two Highland cattle were released, in 1997 and 1998 respectively, as a nature management measure in Westhoek-South. Observations of ponies took place between August 1998 and March 2002. Composition of the herd of Shetland ponies changed during the study period: 25 foals were born in the reserve, one mare was introduced, the first dominant stallion was replaced by another stallion and 15 ponies were transferred to other reserves to avoid overgrazing. In August 1998 there were seven mares with foals and one stallion. In March 2002, 19 ponies were grazing in Westhoek-South: 9 females (6 lactating mares, 1 non-lactating mare and 2 fillies) and 10 males (1 dominants stallion, 3 geldings, 2 yearling males and 4 colts) (Table A.6).

Data of the foraging behaviour of the Highland cattle were collected during August 2001 and March 2002. During that period one cow and three bulls (two of them are offspring of the cow) made up the cattle group.

Houtsaegerduinen

In the Houtsaegerduinen a herd of donkeys graze all over the reserve (total area 80 ha). The site is mainly occupied by *Hippophae rhamnoides/Ligustrum vulgare* scrub, with relatively small and scattered patches of dune grassland and moss-dominated dune vegetation. Old, deteriorating *Hippophae* scrub is generally replaced by species-poor grassland dominated by *Calamagrostis epigejos*. Part of the area has been planted with *Alnus glutinosa* and several non-native tree species (*Populus* div. spp.).

As a nature management measure five donkey mares and one donkey stallion were released in the area in April 1997. Data of field observations of the donkeys integrated in this PhD were collected over a time span of three years (August 1998 – July 2001). At the start of the observations the herd consisted of five adult mares, one adult stallion and two foals. One more mare was introduced in 1999 and 15 foals were born in the reserve. In July 2001 12 female donkeys (7 lactating mares, 2 non-lactating mares and 4 fillies) and 9 male donkeys (3 adult stallions, 3 yearlings and 3 colt foals) were grazing in the Houtsaegerduinen (Table A.6).

Ghyvelde

In Ghyvelde (ca. 75 ha) a herd of Haflinger horses is grazing the entire area. Two thirds of this area is open habitat formed by *Carex arenaria*-dominated grassland, alternating with moss-dominated vegetation (*Hypnum cupressiforme* var. *lacunosum, Dicranum scoparium* and *Polytrichum juniperinum* are among the most prominent moss species). One central forest and several dispersed, small congregations of trees shape the woodland at the site, which is mostly afforested. Approximately 7% of the area is taken by spontaneous scrub of *Hippophae rhamnoides, Ligustrum vulgare, Salix repens* and *Sambucus nigra*.

Observations of the Haflinger horses used in this PhD took place between May 2000 and April 2001. At the initiation of the observations in Ghyvelde the herd of Haflinger horses was composed of four stallions, 11 mares and three foals. Composition of the herd changed twice, but during most of the observations 12 adult horses (three stallions, nine mares) and two foals were grazing the area.

Vegetation units

During observations we recorded the vegetation type where the focal animal was located. It was coded according to Provoost & Hoffmann (1996). This code is primarily based on vegetation physiognomy (forest, scrub, grassland, ...) and on the the dominant plant species. Accompanying species were also noted, e.g. species that influence vegetation structure. This recording of the vegetation type was appointed to the scale of the patch where the animal was located. For data processing we lumped several vegetation types into higher order vegetation units, depending on vegetation structure and assumed relevance to large herbivores, i.e. open vegetation and moss dunes, grassland, rough grassland, rough vegetation, grassland with shrub invasion, scrub and woodland. Most of these vegetation units are present in all study areas, but differ in some aspects in the different areas. Table 1.3 gives an overview of the distinguished vegetation units, their characteristics and their cover in the different areas, as also described below (see also Maps A. 1-4, Appendix). Main species of open (i.e sparsely vegetated) vegetation are *Carex arenaria, Festuca juncifolia* or *Ammophila arenaria*. Mosses and lichens are the main constituants of so-called moss dunes. In Westhoek-South and Houtsaegerduinen, dry dune grassland with *Poa pratensis, Avenula pubescens, Veronica chamaedrys, Galium verum* are part of the 'grassland' type, as well as the *Holcus lanatus* grasslands. Grasslands with *Arrhenatherum elatius* as main graminoid are also part of the grassland type in Houtsaegerduinen. *Carex arenaria* dominates the grassland type in Ghyvelde. Rough grassland, only present in Westhoek-South and Houtsaegerduinen, is formed by the species-poor grasslands dominated by *Calamagrostis epigejos*. Additionally, the wet patches occupied by *Juncus subnodulosus* whether or not accompanied by *Lysimachia vulgaris*, *Lythrum salicaria* or *Mentha aquatica,* are part of the 'rough grassland' in Westhoek-South. Rough vegetation is characterized by tall forbs such as *Eupatorium cannabinum, Cirsium arvense, Lythrum salicaria* and *Iris pseudacorus* in

Westhoek-South, *Eupatorium cannabinum, Cirsium arvense* and *Urtica dioica* in Houtsaegerduinen and *Urtica dioica* in Ghyvelde. Vegetation entities formed by *Rosa pimpinellifolia,* only present in Westhoek-South and Houtsaegerduinen, are also classified as 'rough vegetation'. Where shrub species invade the grassland entities the vegetation evolves into grassy patches with young scrub of mainly *Hippophae rhamnoides, Ligustrum vulgare* or *Salix repens,* i.e. 'grassland with scrub invasion' (only present in Westhoek-South and Houtsaegerduinen). Main shrub species in the three reserves are *Hippophae rhamnoides, Ligustrum vulgare* and *Salix repens*. In Westhoek-South *Crataegus monogyna* and *Prunus spinosa* are additional important shrub species. *Sambucus nigra* is an important shrub species in Ghyvelde. Poplar species are part of the woodland in all three reserves. *Ulmus minor* and *Alnus glutinosa* are additional tree species in Westhoek-South and Houtsaegerduinen.

Outline of the thesis

Chapter 2 focuses entirely on the foraging behaviour and habitat use of different large herbivores, grazing in coastal dune areas. Three different parts, each related to different herbivores, are distinguished: Haflinger horses, Highland cattle & Shetland ponies and Donkeys are the study subjects of part 2.1, 2.2 and 2.3, respectively. In all three parts we investigated how the grazing activity varied within the spatial and seasonal heterogeneity of the study areas. In the work on donkeys we enclosed the changes in foraging behaviour over a period of three years. Additionally, in the case of the cattle and ponies and the donkeys we discussed the potential role of the herbivores in relation to the nature conservation objectives. Non-foraging behaviour was included in the study of the Haflinger horses. In **Chapter 3** we explore differences in grazing behaviour between reproductive and non-reproductive mares in both donkeys and Shetland ponies. **Chapter 4** deals with the question whether free-ranging horses perform latrine behaviour or simply defecate where they graze.

The impact of the observation method on reported time budgets and habitat use of free-ranging equids is investigated in **Chapter 5**. All observational data used in this thesis were collected through continuous focal animal sampling as described by Altmann (1974). This method of sampling provides detailed data on time budgets and habitat use of the observed animals. The extensive data set is a valuable point of departure to compare the technique of continuous focal animal sampling with the less time consuming technique of instantaneous sampling (scan sampling). We investigated whether instantaneous sampling with a given time interval and continuous sampling showed differences in the estimate of time budget and habitat use of free-ranging equids.

(Possible) solutions to the raised hypotheses are compiled in **Chapter 6**. Can this field study provide insights in the underlying mechanisms of foraging behaviour of large herbivores? What is the relevance of our findings for nature management with large herbivores in coastal dunes? What do our results suggest about differences in foraging behaviour between equid species and breeds?

Data sources

Research results are based on observational data collected by several persons. Besides the field data of my own, the observational data of two 'licentiate' (i.e. Master in Science) students, who were supervised by me, were included. Additionally, I incorporated the field data of four students who had done their licentiate thesis in a period preceding (1998-1999) this PhD research or during the beginning of it (1999-2000). These persons are all co-authors of the manuscripts in which their data were incorporated.

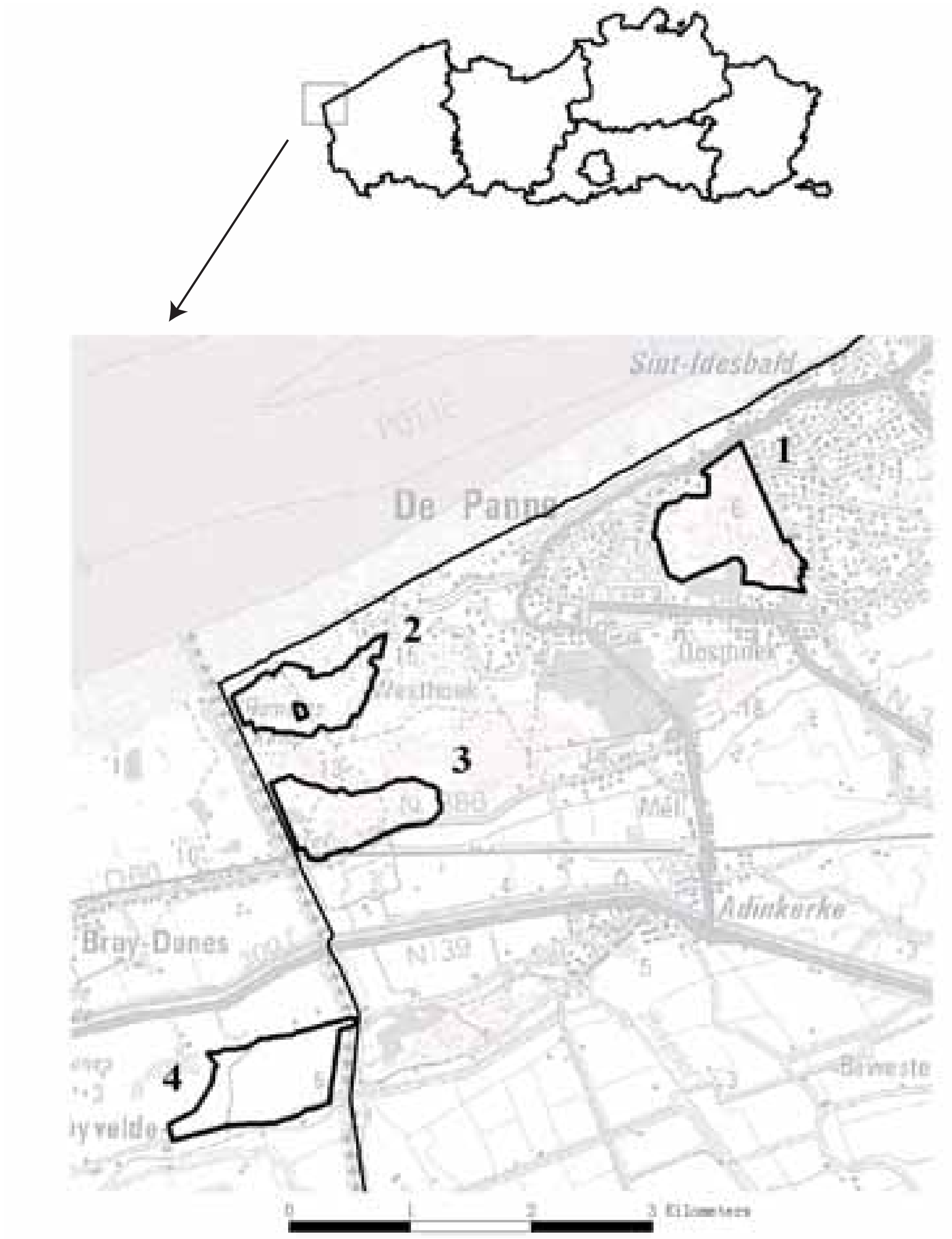

Figure 1.1
Geographical location of the different study sites.
1: Houtsaegerduinen, 2: Westhoek-North, 3: Westhoek-South, 4: Ghyvelde

Table 1.1

Seasonal standing crop of grasslands in the dune system compared with production figures of some managed grasslands in temperate climate.conditions.

Source 1: unpublished data Cosyns

Mean seasonal standing crop of graminoids and herbs of the grassland types in Houtsaegerduinen (HS) and Westhoek-South (WS) under grazed conditions

[a] the different grassland types included are grassland, rough grassland and rough vegetation as described in Table 1.3

2: Ternier et al. 2001

Sum of above ground production of the first cut (spring or early summer) and regrowth (up to October in two or three cuts) of agriculturally managed grasslands dominated by *Poa trivialis, Lolium perenne, Elymus repens, Agrostis sp.* and/or *Alopecurus pratensis* with different fertilizing regimes in the province of West-Flanders (W-Vl), Belgium

3: Morrison et al. (1980, cit. in Radcliffe & Baars (1987))

Annual yields from ryegrass swards in the UK, receiving 450 kg N ha-1 yr-1 (range and average in g DM m^{-2} yr^{-1})

4: Radcliffe & Baars (1987)

Annual yields of pastures receiving phosphor fertilizer 'as required' (average in g DM m^{-2} yr^{-1})

Source		System	Vegetation	Area	Biomass	
					g/m^2	%live
1	Dunes	Grassland types [a]	HS	Summer	368	93
				Autumn	291	85
				Winter	227	26
				Spring	236	63
			WS	Summer	313	74
				Autumn	307	87
				Winter	224	8
				Spring	240	86
2	Agriculture	Grassland with high level of fertilizers	W-Vl	Total	1410	
		Grassland with intermediate level of fertilizers	W-Vl	Total	1170	
		Grassland without fertilizers	W-Vl	Total	950	
3	Agriculture	Ryegrass grassland	UK	Total	(610- 1430) 1140	
4	Agriculture	Pasture	NZ	Total	1040	

Table 1.2

Range and average values of crude protein and NDF of some graminoids, herbs and woody plants in the dune systems Houtsaegerduinen and Westhoek in the different seasons, compared to those of graminoids and herbs in agricultural grasslands. Crude protein contents (CP) and Neutral Detergent Fibre (NDF), expressed as proportion of dry matter.

Source

1: unpublished data Cosyns, see for detailed information Table A.5

Sampled graminoids (they were not all sampled every season): *Ammophila arenaria, Agrostis stolonifera, Arrhenatherum elatius, Carex arenaria, Carex sp, Calamagrostis epigejos, Festuca juncifolia, Holcus lanatus, Juncus subnodulosus, Juncus sp, Poa trivialis, Poa sp.*

Sampled herbs (they were not all sampled every season): *Anthriscus caucalis, Chelidonium majus, Cirsium arvense, Claytonia perfoliata, Eupathorium cannabinum, Galium aparine, Hieracium umbellatum, Rubus caesius, Urtica dioica*, mix of herbs.

Sampled woody plants (they were not all sampled every season): *Fraxinus excelsior, Rosa canina, Rosa pimpinellifolia, Salix repens.*

2: NRC, 1989 and http://eesc.orst.edu/agcomwebfile/edmat/html/pnw/pnw503/composition.html

Graminoids: *Lolium perenne, Phleum pratense, Poa pratensis* (NDF values are only from *Phleum pratense*)

Herbs: *Trifolium repens, Trifolium pratense*

Source	System	Plants	Season	CP (%)		NDF (%)	
				range	avg	range	avg
1	Dunes	Graminoids	Summer	3.6 – 12.6	9.6	32.2 - 76.4	61.1
			Autumn	7.2 – 18.4	13.1	48.3 – 73.7	58.8
			Winter	3.7 – 19.4	8.7	46.6 – 78.2	68.3
			Spring	7.1 – 17.0	12.6	54.2 – 75.8	61.9
		Herbs	Summer	9.1 – 15.6	11.2	32.2 – 52.6	44.5
			Autumn	8.3 – 26.9	15.8	25.3 – 54.7	39.3
			Winter	17.0 – 21.4	19.2	22.9 – 40.0	31.4
			Spring	10.1 – 18.2	14.1	25.5 – 47.8	35.8
		Woody plants	Summer	5.7 – 12.4	9.3	33.6 – 58.6	48.3
			Autumn	6.7 – 8.5	7.6	35.0 – 56.3	47.1
			Winter	6.0	6.0	58.1	58.1
			Spring	6.9	6.9	47.0	47.0
2	Agriculture	Graminoids	Early vegetative	12.2 – 19.0	16.2	55.7	55.7
			Hay	8.6 – 10.8	9.4	61.4	61.4
		Herbs	Early vegetative	22.3 – 25.9	24.0	26.7	26.7
			Hay	15.0 – 22.4	18.7	36.0 – 46.9	41.4

Table 1.3

Area, description and dominant plant species of the vegetation units distinguished in the study sites Westhoek-South, Houtsaegerduinen and Ghyvelde

Vegetation unit	Cover (%)	Area ha	Description and dominant species
Open vegetation & Moss dunes			sparse vegetation cover with *Carex arenaria, Festuca juncifolia* or *Ammophila arenaria* vegetation cover provided by mosses and lichens
Westhoek -South	11.0	6.6	
Houtsaegerduinen	7.8	6.3	
Ghyvelde	32.0	24.3	
Grassland			
Westhoek -South	9.4	5.6	species rich dune grasslands + moist *Holcus lanatus* grasslands
Houtsaegerduinen	4.7	3.8	species rich dune grasslands + grasslands with *Holcus lanatus* and/or *Arrhenatherum elatius*
Ghyvelde	35.0	26.5	*Carex arenaria* - dominated grasslands
Rough grassland			
Westhoek -South	7.7	4.6	species-poor grasslands dominated by *Calamagrostis epigejos* + wet patches occupied by *Juncus subnodulosus*
Houtsaegerduinen	4.1	3.3	species-poor grasslands dominated by *Calamagrostis epigejos*
Rough vegetation			
Westhoek -South	9.1	5.5	vegetation dominated by *Rosa pimpinellifolia* + vegetation dominated by tall forbs such as *Eupatorium cannabinum*, *Cirsium arvense, Lythrum salicaria* or *Iris pseudacorus*
Houtsaegerduinen	3.5	2.9	vegetation dominated by *Rosa pimpinellifolia* + vegetation dominated by tall forbs such as *Eupatorium cannabinum*, *Urtica dioica* or *Cirsium arvense*
Ghyvelde	3.0	2.3	vegetation dominated by tall herbs, mainly *Urtica dioica*
Grassland/Shrub			grassland in which young scrub of mainly *Hippophae rhamnoides, Ligustrum vulgare* or *Salix repens* appear
Westhoek -South	7.1	4.2	
Houtsaegerduinen	2.0	1.6	
Scrub			main shrub species:
Westhoek -South	41.3	24.8	*Hippophae rhamnoides, Ligustrum vulgare, Salix repens, Crataegus monogyna,Prunus spinosa*
Houtsaegerduinen	67.0	54.4	*Hippophae rhamnoides, Ligustrum vulgare, Salix repens*
Ghyvelde	7.0	5.3	*Hippophae rhamnoides, Ligustrum vulgare, Salix repens, Sambucus nigra*
Woodland			main tree species:
Westhoek -South	14.4	8.6	*Populus spec., Ulmus minor, Alnus glutinosa*
Houtsaegerduinen	10.8	8.8	*Populus spec., Ulmus minor, Alnus glutinosa*
Ghyvelde	23.0	17.4	*Populus spec.*

Note: for analyses in Chapter 3 Grassland, Rough grassland, Open vegetation and Moss dunes were lumped together in the vegetation unit 'Grassy vegetation'; for analyses in Chapter 5 Open vegetation and Moss dunes were incorporated in the vegetation unit 'Grassland' Westhoek-North is not mentioned in the table, since data of Westhoek-North were only used in Chapter 4 (Eliminative behaviour) where we did not use the level of vegetation units but the level of vegetation types

2

FORAGING BEHAVIOUR AND HABITAT USE OF FREE-RANGING LARGE HERBIVORES

2.1. Do season and habitat influence the behaviour of Haflinger mares in a coastal dune area?

Lamoot Indra, Hoffmann Maurice

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Haflinger horse, Ghyvelde (foto: Indra Lamoot)

Abstract

This study was performed to gain more knowledge about the behaviour and habitat use of Haflinger mares, free-ranging in a low-productivity dune area. Detailed data on these animals' time-budgets were collected over a full year, through the focal animal observation technique. On average the Haflinger horses spent 68% of the daytime grazing, 18% resting and 8% walking. The horses' behaviour was significantly different among seasons, mainly through a change in grazing time. Shorter grazing times in summer allowed the animals to rest longer than during the other seasons. We suggest that especially the decreased forage quality and quantity of the grazed habitats in the non-growing season accounted for the increased grazing time in autumn and winter. In all four seasons the horses preferred grazing in the grassy habitat. However, habitat use showed seasonal variation. Moss dunes were grazed more intensively in winter and spring, compared to summer and autumn. Throughout the year rough vegetation, scrub and woodland were little grazed. For several response variables the observed variation could be partly explained by the differences between individual animals.

Keywords: horse, free-ranging, habitat use, time-budget, grazing behaviour, non-grazing behaviour.

Introduction

Several authors have reported (daylight or 24 hours) time-budgets of feral horses (Salter & Hudson, 1979; Jarrige & Martin-Rosset, 1987) or free-ranging horses living in natural or semi-natural conditions (Duncan, 1980, 1985; van Dierendonck et al., 1996; Berger et al., 1999; Boyd & Bandi, 2002). On the whole, time-budgets of free-ranging and feral horses show large similarities, with highest time-investment in grazing. Resting, moving and alertness take most of the remaining time. However, behavioural differences due to environmental conditions, such as habitat, forage quality and weather are reported, as well as a relationship with intrinsic aspects such as age, sex and reproductive state.

The aim of the present study was to describe the behaviour and the habitat use of Haflinger horses, introduced into an old coastal dune area with low primary production. This low-productivity environment offers the herbivores rather low levels of forage quality and quantity, in comparison with more nutrient rich systems. These nutrient and energy restrictions are even more pronounced during the non-growing season (Bokdam & WallisDeVries, 1992; Duncan, 1992), i.e. the season with low plant production (from October to March in temperate regions). Free-ranging herbivores have 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. These decisions are primarily made in relation to forage availability and quality, which are in turn determined by environmental conditions. We expect that the rather low levels of forage quality and quantity will be reflected in the foraging behaviour of the Haflinger horses, in particular by long grazing times. Furthermore, we suppose that the horses adjust their behaviour and habitat use to the seasonal changes in their environment. According to the literature we may assume that this adjustment will result in an increased grazing time as well as a broader habitat use outside the growing season (e.g. Pratt et al. 1986; Duncan, 1983; Duncan, 1985).

Material and Methods

Study site and animals

Research was performed in the nature reserve Ghyvelde (60 ha), an old dune area close to the northern French coastline and bordering an equally old dune ridge in Belgium (Adinkerke). Ghyvelde is located in a coastal region with mild winters and mild summers. Mean annual temperature is 9.8°C. In summer, autumn, winter and spring mean temperature is 15.9°C, 10.8°C, 3.9°C and 8.7°C, respectively, mean monthly precipitation is 60.7mm, 74.8mm, 56.5mm and 48.5mm, respectively (means over the period 1963-2002) (Meteo WVL vzw).

Two thirds of the area is covered by open habitat, mainly formed by *Carex arenaria*-dominated grassland (*Plantagini-Festucion* community), alternating with moss dunes, dominated by mosses and lichens and a sparse cover of grasses and forbs (*Thera-Airion* community). One central afforested area and several dispersed, small patches of trees shape the woodland at the site (approximately 23% of the area). Approximately 7% of the area is scrub vegetation, consisting of *Hippophae rhamnoides, Ligustrum vulgare, Salix repens* and *Sambucus nigra*.

During the study, a herd of 14 to 18 Haflinger horses grazed the site. They were introduced to decrease or hamper the encroachment of competitive plant species that tend to form species poor to monospecific vegetations. They graze year round and no additional food is given. The horses have access to one artificial water point for drinking. We chose three adult mares as the focal animals for the observations: one had a foal, the other two were non-lactating. All three mares were in good condition.

Behavioural observations

Data were collected through continuous focal animal observation (Altmann, 1974). From May 2000 until April 2001 we conducted 31 sessions of six hours (with a frequency of 3 sessions per month). All observations took place during daylight (between 9:00h and 19:00h) and were done by one observer. During a six-hour period we continuously monitored the behaviour of one focal animal, chosen at random from the three mares that were a priori selected for this study. Most of the horses are habituated to humans and can be approached within a range of 1 m without causing any visually observable influence on behaviour.

We recorded the duration (accuracy: 1 s) of the different behavioural types, as well as the vegetation type and the vegetation height. We recorded and took into account grazing as well as non-grazing behaviour (drinking, walking, standing alert, resting upright, laying down, rolling, grooming, mutual grooming, defecating, urinating). To analyse the data the different vegetation types considered in the field were lumped into five habitat types: 'grassy vegetation', 'moss dune', 'rough vegetation', 'scrub' and 'woodland', which cover 35%, 32%, 3%, 7% and 23% of the area respectively. For vegetation height 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'. We have no data on the relative availability of each of these height classes. 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).

Data analysis

The calculation of the time-budget was based on the total time spent per day on each behaviour. Variation in the time-budget was investigated by the use of the following response variables: mean time per day spent in a certain behaviour, mean number of bouts, mean number of periods of a certain behaviour per day, mean duration of a bout and mean duration of a period of a certain behaviour. A "bout" is a phase in which a certain behaviour is performed without interruption. A "period" is the accumulation of several bouts of the same behaviour if they are not interrupted for more than five minutes. For example, the horse can stop a grazing bout to scan its environment. After a few seconds or minutes it can prolong its grazing behaviour and stop this to start a resting period. That grazing period (called a "meal") consists of two grazing bouts. The short interruption is not seen as a break of the meal, but is not included in the calculation of the meal duration, which is only the effective grazing time during a meal. Main attention focussed on the behavioural types grazing, resting and walking. Additionally, we considered standing alert, grooming, mutual grooming, drinking, defecating, urinating and rolling. We investigated whether the observed variation in the response variables was affected by seasonality. We were aware of the possibility that differences in behaviour between individual animals could explain, at least partly, the observed variation. Therefore, we used mixed-model ANOVA to investigate the effect of the fixed factor 'season' on the variation in mean time, mean number of bouts and mean bout duration, and included the random factor 'individual' into the model. If the random factor was not significant, we consequently excluded it from the model. The Scheffé multiple comparison procedure was used as post hoc test. In case of inconsistency with the assumptions for the use of ANOVA, we used Kruskal-Wallis One Way Analysis. However in such cases we could not incorporate a random factor. This meant that for the analysis of the effect of the factor 'season', the impact of possible individual differences could not be regarded. Hence, we had to analyse the potential effect of 'individual' with a separate analysis.

To investigate the habitat use of the horses we considered the variable mean grazing time per day per habitat type or per vegetation height. When on a given day an animal was not grazing in a certain habitat or height, null values were included to calculate the mean grazing time. In the ANOVA-model we considered two fixed factors 'season' and 'habitat type' or 'height category', their interactions and the random factor 'individual'. We eliminated a non-significant random factor or interaction from the final model. We investigated the use of the five different habitat types a second time by taking into account the availability of the five habitat types. Therefore we divided the mean grazing time per day per habitat type by the available surface (in ha) of that habitat type.

All analyses were performed using SPSS 11.0 for Windows.

Results

Time-budget

Table 2.1.1 gives an overview of the time budget of the three Haflinger mares. In general grazing took the main part of the time-budget; on average 68% of the observed time. On average, the horses spent 18% of their daytime resting, 8 % walking and 3% standing alert. Grooming, drinking, nursing, mutual grooming, defecating, urinating, rolling and interactions accounted for only 4% of the total daytime. Fig. 2.1.1 illustrates the time-budget over the whole year and the variation between seasons.

Grazing behaviour and habitat use

Mean grazing time per day was affected by season ($p=0.030$). The random factor individual could not be deleted from the statistical model as it had a significant effect. Post-hoc tests showed that the horses had significantly lower grazing times in summer compared to autumn and winter (Su: 56% of six hours; Au: 71%; Wi: 78%; Sp: 68%).
Average duration of a meal, average duration of a grazing bout, average number of meals and average number of grazing bouts were not different in the four seasons. However, the observed variation in meal duration, grazing bout duration, number of meals and number of grazing bouts could be explained to a certain extent by the differences between individual animals.
To investigate the habitat use of the horses we considered the differences in average grazing time per habitat type per day. The horses grazed 176 min/6 hrs in grassy vegetation and 54 min/6 hrs in moss dunes. In comparison, grazing times in other habitat types were much lower: 2, 7 and 4 minutes in rough vegetation, scrub and woodland respectively. Table 2.1.2a illustrates the ANOVA results: significant main effect of habitat ($p<0.001$), significant interaction season*habitat ($p<0.001$) and a significant random effect.
Similar results were found when we analysed the habitat use taking into account habitat availability (grazing time in grassy habitat: 6.50 min/6 hrs/ha; moss dune: 2.50 min/6hrs/ha; rough vegetation: 0.85 min/6hrs/ha;

scrub: 1.32 min/6hrs/ha; woodland: 0.30 min/6hrs/ha) (Table 2.1.2b; Fig.2.1.2). The significant interaction illustrates the seasonal changes in habitat use. Moss dunes were grazed more in winter and spring than in summer and autumn, and this was at the expense of the grassy habitat. Rough vegetation was only foraged in autumn. In autumn, winter and spring scrub was grazed a bit more, compared to summer. The woodland was visited for grazing a bit more often in spring, compared to the other seasons. Nonetheless, the horses foraged less in rough vegetation, scrub and woodland, throughout the year.

We analysed the effect of vegetation height on grazing time when the horses were foraging in grassy habitat and moss dune. The Haflinger mares were grazing in hoof high vegetation 57% of the time that they were grazing in grassy habitat or moss dune, and 40% in shortly grazed vegetation. This difference seemed more pronounced in summer and spring than in autumn and winter, so we also analysed if there was a significant interaction between the effect of height and the effect of season. There was a significant effect only of height (p=0.029). No significant interaction or significant random effect of individual was found.

Resting behaviour

The mean resting time per day was significantly different between seasons (p=0.005) and between individual animals. In summer significantly more time was spent resting compared to autumn, winter and spring (result of post hoc-tests) (Su: 27% of six hours; Au: 13%; Wi: 12%; Sp: 17%). The duration of a resting period and the duration of a resting bout were similar in all seasons and for all individuals. The factor season had also no effect on the average number of resting periods. Number of resting periods and number of resting bouts were significantly different between individual animals. Resting behaviour was only observed in grassy vegetations and moss dunes, never in rough vegetation, scrub or woodland.

Walking behaviour

The mean walking time per day was not affected by the factor season. In summer, autumn, winter and spring the Haflinger mares on average walked respectively 33 min, 30 min, 24 min and 22 min/6 hours. Individual horses did not differ in mean walking time per day. There were no seasonal or individual differences in the average duration of a walking period, average number of walking periods, average walking bout and average number of walking bouts. Horses mostly walked in the grassy vegetations and moss dunes, and rarely moved around in rough vegetation, scrub or woodland.

Other behavioural aspects

We considered here the behaviours standing alert, grooming, mutual grooming, drinking, urinating, defecating and rolling. We found no seasonal variation in the mean time per day spent on these behaviours. For the behaviours standing alert and rolling we found significant individual differences. The mean grooming frequency per day was significantly different between seasons (p=0.004) and between individuals. Individual variation was also found for the mean defecating frequency. The mean time of a bout was different between seasons for defecating and different between individual horses for grooming.

Discussion

Time-budget

On average, the Haflinger horses spent 68% of the daytime grazing and 18% resting, of which only 1% was lying down. The horses were walking around for 8% of their time and spent 3% standing alert. This daylight time-budget is in line with time-budgets of other free-ranging and feral horses. Jarrige & Martin-Rosset (1987) reported that feral horses spend 50-73% of their time grazing during daylight. Przewalski horses in a nature reserve in the Mongolian steppes only grazed 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 and resting 20-30%, the remainder being spent on alertness and movement. We suggest that the rather long grazing times of the Haflinger horses reflect the poor nutritive quality and quantity of the grazed habitats. Berger (1986) reported long grazing times (68.3% & 78.1% for non-reproductive and reproductive mares) in low quality home ranges as opposed to lower grazing times (58.5% & 65.8% for non-reproductive and reproductive mares) in high quality home ranges.

We found low daily resting times, and resting occurred mainly in the standing position. As Duncan (1985), Mayes & Duncan (1986) and Pratt et al. (1986) already indicated for other horse breeds, we consider it very probable that the Haflinger horses also rest more at night, in the standing as well as in a recumbent position, than during the day. Paradoxical sleep occurs in the recumbent resting periods (Boyd, 1998; Waring, 2003); however, standing, not recumbency, is the posture of minimal energy demand for horses (Winchester, 1943). Environmental factors influence the horse's resting behaviour (Waring, 2003), while individual variation has been reported as well (Duncan, 1980). However, we believe that there is a minimum level for resting critical to equid well-being, as also suggested by Duncan (1992). Increased resting time above this threshold is possible when other maintenance requirements are fulfilled. In nutrient poor systems horses will be more time-limited, in comparison with horses in nutrient rich systems, owing to the increased foraging effort needed to meet their energy and nutrient requirements. We suggest that on the one hand the maximum grazing time of horses is determined by a threshold for other maintenance activities, in particular resting. On the other hand "free" time to increase the resting time is mainly determined by the time spent on the horses' main activity, i.e. grazing. Since the Haflinger horses forage in a low productive, nutrient poor system, we hypothesize that even if the horses rest more at night, the proportion of the time spent resting in a 24-hour period would remain low, in comparison with other studies (Duncan, 1985; Boyd, 1998). Furthermore, diet is one of the factors affecting patterns of sleep. Stabled horses increased their total time lying down when fed on a higher quality diet (Dallaire & Ruckebush, 1974). Duncan (1985) found a positive correlation between time spent lying and protein concentration in the diet. The Haflinger horses were mainly foraging on grassland dominated by *Carex arenaria*, which has indeed a low protein content, especially in the non-growing season (Cosyns, unpubl.).

Seasonal variation in time-budget

During the autumn and winter the horses increased their grazing time, while in summer feeding time dropped to a minimum. This is in line with previous studies in temperate regions (Duncan, 1985; van Dierendonck et al., 1996; Berger et al., 1999; Cosyns et al., 2001; Menard et al., 2002), as well as in subarctic conditions (Salter & Hudson, 1979). We suggest that the relatively higher quality and availability of forage in summer accounted for the drop of grazing time compared to the non-growing seasons. Horses perform most of their foraging behaviour during the daylight period (Duncan, 1985; Pratt et al., 1986). Therefore, we might expect that in autumn and winter the grazers had to concentrate their grazing more in a shorter daylight period, than in summer and spring, when they can spread their grazing activities over a longer daylight period. Although this could partly explain the increased daylight grazing time in autumn and winter, we also find this pattern in studies which have calculated time-budgets based on observations spread over twenty-four hour periods (Duncan, 1985; Berger et al., 1999; Menard et al. 2002). Thermoregulation during hot summer days could result in more grazing during the late evening or night. However, we rarely observed horses seeking shade. Therefore we assume that this factor was of minor importance in explaining the seasonal variation in daylight grazing time. Some authors have suggested that the observed drop in foraging time in summer is mainly caused by a response to attacks by biting flies (Duncan, 1985; Mayes & Duncan, 1986), which is also seen in reindeer (Hagemoen & Reimers, 2002). Though we did not measure this variable, we think that biting insects are not present at the study site in such numbers that they would influence the horses' behaviour strongly. The lack of seasonal variation in grazing bout duration and number of grazing bouts could reflect the lack of disturbance by external factors, such as biting flies. Concluding, as mentioned above, we suggest that seasonal differences in forage quality and quantity play a major role in the seasonal variation in grazing time of the Haflinger mares in the present study. Grazing time is generally lowest when forage is abundant and of good quality, and highest when forage is of low quality or availability is limited (Vallentine, 1990; Stuth ,1991). Duncan (1985) suggested that horses increased their feeding time in winter to a maximum possible value in an attempt to maintain a high quality diet. Lamoot *et al.* (this PhD.) found longer grazing times, but lower bite rates, in autumn and winter compared to summer and spring, for donkeys and ponies. At the level of the grazed patch, a prolonged searching time for plants or plant parts to be consumed to achieve a diet of acceptable quality, might increase the grazing time (and diminish the bite rate).

The Haflinger horses in the present study spent more time resting per day in summer, in comparison with the other seasons, mainly as a result of the (non-significantly) higher number of resting periods in summer. There was no seasonal variation in walking time per day. As discussed above, we assume that the increased resting time in summer was related to the decreased grazing time in summer. In summer the grazing horse could meet its nutritional requirements more easily and in less time. Consequently, this resulted in “free” time available to spend resting. Seasonal variation in resting time and the lack of seasonal variation in walking time are not in line with the findings of Duncan (1985). He found longer walking times in summer, and little seasonal variation in time spent resting. This might be due to the differences between study sites. In our study site palatable patches are available in a more or less continuous pattern. Therefore, seasonal variation in walking time is not expected. In the Camargue insect harassment in summer could result in more moving around. We suggest that insects are not present in our study site in such numbers that they would influence the horses’ behaviour strongly.

Seasonal variation in grooming frequency per day was found, with more grooming bouts in spring, which could be related to the moulting season, as was also suggested by Tyler (1972). We did not find differences between seasons for any of the other behaviours considered. Mean frequency of drinking at Ghyvelde was 2.1 time per 6 hours. Feral horses are reported to drink only once or twice in a 24 h period (Fraser, 1992). At pasture, frequency, but not duration of drinking bouts increased as temperature increased (Crowell-Davis *et al.*, 1985), a phenomenon not found in the present study. Kimura (1998) reported seasonal variation in mutual grooming, probably due to changes in distances between individual horses. No seasonal differences in mutual grooming behaviour were found in the present study.

Although we did not measure distances between horses, our field observations did not indicate remarkable seasonal changes in individual spacing.

Habitat use

Taking in account the availability of the distinguished habitat types, we found that the horses grazed predominantly in grassy habitat, i.e. the grasslands dominated by *Carex arenaria*. However, the habitat use of the Haflinger horses showed seasonal variation. In winter and spring moss dunes were grazed longer than in summer and autumn. The grassy habitat was grazed less in winter and spring. Rough vegetation, scrub and woodland were little grazed throughout the entire year, although there was a limited use of scrub that remained constant over the entire year. A slightly increased use of rough vegetation was observed in autumn, and woodland was used a little more in spring. When grazing grassy habitat and moss dune, the mares grazed significantly more in patches with 'hoof' height, compared to shortly grazed patches. This figure did not provide any indications on preferences, however, as there are no data about the relative availability of the different vegetation heights. We hypothesized that the Haflinger horses would show seasonal variation in habitat use, which is confirmed by our results. However, we expected that the horses would graze more in scrub and woodland during the non-growing season, due to the expected depletion of the preferred grassy habitat. It remains unclear why the Haflinger horses did graze more in moss dunes, and not in woodland or in scrub. A possible reason could be the presence of a relatively large number of winter annuals in these moss dunes, which might serve as relatively good quality winter forage. However, there are no data on the total primary production and nutritive quality of these winter annuals to support this suggestion. Our results are in line to some extent with the findings of Gordon (1989), who investigated vegetation community selection on the Isle of Rhum (Scotland). Out of four different ungulates (cattle, red deer, goat and pony) ponies performed the smallest seasonal changes in vegetation use. Only in autumn ponies broadened their vegetation community use. Pratt et al. (1986) reported that grasslands remained of major importance throughout the year for New Forest ponies, which is consistent with our results, but the ponies showed a greater flexibility in foraging behaviour over the winter months. Especially woodland was grazed more in winter. Also Duncan (1983) concluded that the Camargue horses were more dispersed over the various vegetation complexes in the cooler season.

Variation among individual horses

In the Camargue the time-budgets of free-ranging horses were investigated over several years (Duncan, 1980). Based on differences in time spent standing resting, standing alert and lying down, he could divide the animals into three groups, i.e. adult females, yearlings and adult males. The time spent foraging and walking was remarkably similar for all the individuals. Prior to the present study period we selected three adult mares for observation. Consistent with the findings of Duncan (1980) and because the horses were foraging as a herd, we did not expect far-reaching differences in time-budget between the mares. However, for the analysis we wanted to take into account possible variation among individuals, especially because we noticed during observations that one mare, older and presumably high on the dominance rank, was grazing less than the other two. Our results demonstrate that the time-budgets indeed differed between the observed mares. We suggest that bias through individual variation could be avoided to some extent by increasing the number of focal animals for the data collecting through the focal animal observation technique. The individual variation in time-budgets has far-reaching consequences for data analysis. When investigating environmental differences in behavioural aspects, one has to keep in mind that variation between observed individuals can bias the results, if not incorporated in the statistical analyses. Again, we suggest the need for a larger sample size when investigating the behaviour of a herd of horses.

Conclusions

The Haflinger mares performed time-budgets similar to those presented in literature, with grazing as the main time-investment. They showed rather long grazing times, which could be a response to their low productive habitat. The horses' behaviour was influenced by the factor season, mainly through a change in time spent grazing. The drop in grazing time in summer made time available for resting. During the entire year, most of their grazing, as well as their non-grazing behaviour, took place in *Carex arenaria*-dominated grassland with short sward height. In winter and spring moss dunes were grazed more compared to summer and autumn. Although not expected, individual variation explained at least partly the observed variability of many variables.

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Table 2.1.1

Time (minutes) per 6 hours day and number of bouts per 6 hours of each behaviour: mean, minimum (min.), maximum (max.) and Standard Error (SE). Sample size: 3 individuals, 31 observation days. Fixed effect of season and random effect of individual (ind.) on mean time per day and mean number of bouts were investigated: ***: p<0.005; **: p<0.01; *: p<0.05; n.s.: not significant

Behaviour	Time				Effect		Number				Effect	
	Mean	Min.	Max.	SE	Seas.	Ind.	Mean	Min.	Max.	SE	Seas.	Ind.
Grazing	242.6	128.3	291.0	16.1	*	***	92	44	112	5.9	n.s.	n.s.
Resting	63.8	25.5	153.2	12.0	***	***	9	3	29	2.4	n.s.	***
Resting up	59.4	7.3	152.3	12.8			9	2	28	2.5		
Lying down	4.4	0.0	25.8	2.3			1	0	3	0.3		
Walking	27.9	15.5	37.4	2.1	n.s.	n.s.	76	56	91	3.4	n.s.	n.s.
Standing alert	12.3	3.3	33.2	2.9	n.s.	**	25	8	45	4.2	n.s.	n.s.
Grooming	4.0	0.9	9.1	0.8	n.s.	n.s.	11	5	17	1.4	***	***
Drinking	2.0	4.2	4.8	0.4	n.s.	n.s.	2	1	5	0.4	n.s.	n.s.
Mutual groom.	1.4	0.0	6.3	0.6	n.s.	n.s.	2	0	7	0.6	n.s.	n.s.
Defecating	0.8	0.2	1.9	0.1	n.s.	n.s.	4	1	6	0.5	n.s.	*
Urinating	0.6	0.2	1.0	0.1	n.s.	n.s.	3	1	5	0.4	n.s.	n.s.
Rolling	0.1	0.0	0.4	0.0	n.s.	*	0.4	0	1	0.1	n.s.	n.s.
remainder	0.1											

Table 2.1.2

Results of the mixed-models ANOVA examining the effects of the fixed factor 'Habitat type', 'Season', the interaction, and the random factor 'Individual' on the variable Grazing Time. a: without taking into account the availability of the habitat types. b: with taking into account the availability of the habitat types

		df1	df2	F	P
a	Habitat	4	33	152.634	**<0.001**
	Season	3	33	0.880	0.462
	Habitat*Season	12	33	4.347	**<0.001**
	Individual (Random)				significant
b	Habitat	4	33	69.149	**<0.001**
	Season	3	33	1.739	0.179
	Habitat*Season	12	33	2.988	**0.006**
	Individual (Random)				significant

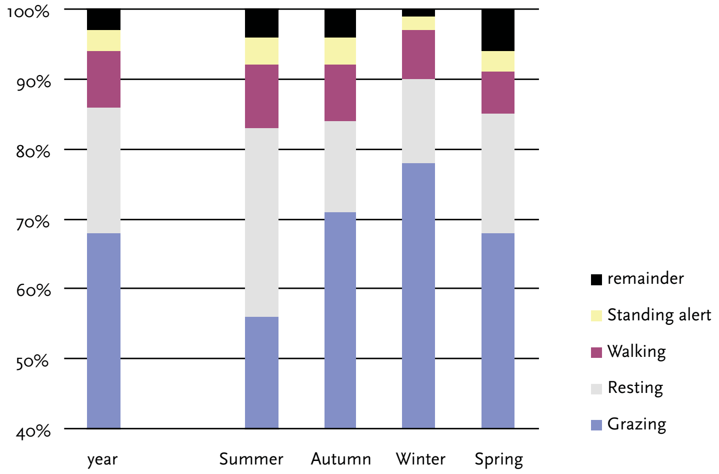

Figure 2.1.1
Time-budget of the Haflinger horses over the entire year, and in summer, autumn, winter and spring. Percentages are based on mean time spent per day.

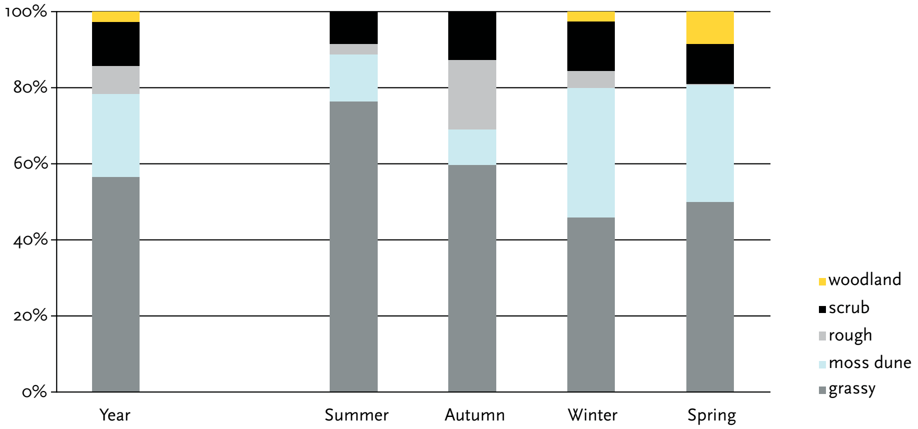

Figure 2.1.2
Habitat use of the Haflinger horses over the entire year and in summer, autumn, winter and spring, taking into account the availability of the habitat types. Percentages are based on mean time grazing per day per ha.

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

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Highland cow, Westhoek-south (foto: Indra Lamoot)

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 poor 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 is 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 between 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 (assuming a sufficient animal density). 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.

Keywords: foraging behaviour, grazing time, diet, habitat overlap, niche breadth

Introduction

In the late 1990's 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 beginning of the twentieth century practically all coastal dunes were grazed for agricultural purposes, 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 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 & Gordon, 1993). Coexisting ungulates tend to use their environment in different ways (Gordon, 1989b), resulting in 'niche differentiation' or 'resource partitioning'.

Shetland ponies and Highland cattle, our study animals, 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, Foose & Robertson, 1983), structure of the incisor arcade (Gordon & 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 &

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 & Van Soest, 1985; Illius & 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 & 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 grazing 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 Cosyns) 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 & 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 (more frequently found in dicotyledons than in monocotyledons) (Freeland & Janzen, 1974), which is unknown for equids.

Material and Methods

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 is occupied by grassy habitat. Within the grassy habitat we distinguished the vegetation units 'grassland', 'rough grassland', 'grassland with scrub invasion', 'rough vegetation' and 'moss dune 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 (85-107 kg ha^{-1}) compared to the range of biomass in near-natural grazing systems in temperate regions (8-67 kg ha^{-1}) (WallisDeVries, 1998).

Behavioural observations

Observational data were collected through continuous focal animal sampling (Altmann, 1974) from August 2001 until March 2002. During a six-hour period (daylight, ranging from 5:30h until 22:30h) 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 minutes 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 visible 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 six-hour 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: 'grassland', 'rough grassland', 'grassland with scrub invasion', 'rough vegetation' and 'moss dune 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).

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*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'. To calculate 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 observation period 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 hour 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 minutes during a six hour 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 arcsine 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:
$D_i = (p_i - A_i)/((p_i + A_i) - (2^* p_i^* A_i))$
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 values indicating avoidance and selection of the habitat type, respectively.
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 / Â p_i?) (Begon, Harper & Townsend, 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 chose Kulczinski's index (_hc) (Oosting, 1956) to measure niche overlap. _hc = Â min(pip, pic) where pip and pic are the proportions of the grazing time that ponies and cattle, respectively, spent in the ith habitat type $_{ype}$ (or vegetation unit or sward height). We also employed these indices to examine forage niche breadth and forage use overlap, with pi being the proportion of the total number of bites taken in the *i*th forage class.

Results

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 2.2.1). Both species had significantly longer 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 between 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).

Habitat use

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 2.2.2). In addition, the interactions Habitat*Species and Habitat*Season were significant. Both species spent most of their foraging activity in the grassy habitat, although the interaction Habitat*Species shows that there existed a difference between both species. 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 (Figure 2.2.1). In all seasons the grassy habitat was an intensively foraged habitat, but seasonal shifts were 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 2.2.3). Throughout the year, woodland was preferred by cattle and avoided by ponies. However, calculated by season, woodland was only preferred in spring. 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 2.2.2). Both species had similar bite rates when foraging in grassy habitat, but ponies grazed faster than cattle in scrub and woodland.

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 ($F_{12,\ 187} = 3.50$; $P < 0.001$). Figure 2.2.2. illustrates the proportion of grazing time spent in the five vegetation units when grazing in grassy habitat, averaged over the four seasons. Both species divided their grazing activity not uniformly over the five vegetation units. Slight differences between both species are visible, but these are not significant. This habitat use was also variable over the seasons[1]. 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 almost not grazed in winter and spring, but were grazed in summer and autumn, which is also reflected in the Jacobs’ index of selection (Table 2.2.3). 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*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 however illustrates that this varied among seasons. The trends were similar for both species.

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 investigated this in grassland, a vegetation unit which was highly preferred by both cattle and ponies (Figure 2.2.2; Table 2.2.3). The results of the ANOVA (Table 2.2.4) 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*Species and Height*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*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 (Figure 2.2.3). We found the same results when we considered the variable ‘proportion of bites’ (Table 2.2.4). When grazing in grassland cattle achieved a higher bite rate than ponies (40 bites/min and 31 bites/min respectively), as indicated by the significant effect of the factor Species on ‘bite rate’ (Table 2.2.4). There were also significant effects of the factors Height and Season, and of the interaction Height*Season. Overall, the herbivores had highest bite rate when grazing in a sward of less than 3 cm, but this was variable among seasons.

Diet Composition

Table 2.2.5 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 at least 10 species of graminoids, 23 species of forbs and 17 woody plant species; that of the ponies consisted of at least 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.

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*Class ($F_{2,\ 158} = 15.42$; $P < 0.001$) and Season*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 2.2.6). 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 2.2.6 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 habitat 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*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 composition 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*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 both species. The cattle increased the proportion of forbs (13.1%) and especially woody plants (22.1%) in their diet. By contrast, the ponies foraging in scrub in autumn only rarely consumed woody plants (0.3%) and forbs (1.1.%).

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 six hour observation period was similar for the two species (cattle: 590 ± 50 m; ponies: 630 ± 31 m) and was not significantly different between seasons.

The high abundance of graminoids in the diet 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 2.2.7 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 lower values are found for the forage use overlap within scrub and within woodland.

Discussion

Grazing behaviour

Ponies spent a lot more time on foraging than cattle, which corresponds with the findings of previous studies (Arnold & Dudzinski, 1978; Arnold, 1984; Menard et al., 2002). During a six-hour period ponies spent, on average, two hours more on grazing than did cattle and they did so in every season. Throughout the year the ponies in the Westhoek achieved long grazing times (70.7% of their time). These long grazing times are not extremes but are situated around the upper limit when compared with other studies. Jarrige & 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 & 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; Duncan, 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 & Dudzinski, 1978; Pratt et al. 1986; Menard et al., 2002).

However, other studies (van Wieren, 1992; Vulink et al., 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, 1992). 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 hour period due to their longer 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.

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 nor 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 & 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 units, unlike the cattle with a decreased bite rate in scrub and woodland. In grassland, rough grassland and rough vegetation cattle grazed faster than ponies. Factors like searching time, handling time and mastication time determine the bite rate (Spalinger & Hobbs, 1992). For example, a decreased bite rate can be the result of an increased searching time, because of less available food items, or an increased browsing activity. In Figure 2.2.4 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. An increased browsing activity certainly explains the decreased bite rate of cattle when foraging in scrub.

In the grasslands, intensely grazed by both herbivores, there was a differentiation in the sward heights used by the two ungulates. In the grasslands the ponies took 46% of their bites from very short swards and 51% 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 & 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 grasslands with very short sward height are not concentrated in the study area 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 bites/min 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 & Gordon, 1987). However, in the Westhoek the cattle maintained a high bite rate on swards with a height of less than 3 cm. A 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 then 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, providing 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 a level of 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 (<7–8cm) although they could have achieved greater intake rates on taller mature patches (WallisDeVries & Daleboudt, 1994; Ginane, Petit & D’Hour, 2003).

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; Cosyns 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 & 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.

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 managment 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 better 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 30% 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 the 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 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, Bonis & Bouzillé, 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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Table 2.2.1

Grazing behaviour of cattle and ponies throughout the year and in the different seasons. Mean values per six hour period ± SE. % of time: proportion of time spent on grazing.

		% 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

Table 2.2.2

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

		Grazing time			Bites			Bite Rate		
	df1	df2	F	P	df2	F	P	df2	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.

Table 2.2.3
Jacobs' index of selection for cattle (C) and ponies (P).
No selection (0): -0.08 < Index < 0.08. Avoidance (-): -0.4 < index < -0.08. Strong avoidance (—): index < -0.4. Preference (+): 0.08 < index < 0.4. Strong preference (++): index > 0.4. Open + Moss: open vegetation & moss dunes; Grassland/Scrub: grassland with scrub invasion

Vegetation	**Area**	**year**		**Summer**		**Autumn**		**Winter**		**Spring**	
		C	**P**	**C**	**P**	**C**	**P**	**C**	**P**	**C**	**P**
Grassland	9 %	++	++	++	++	++	++	+	++	++	++
Open + Moss	11 %	—	-	—	—	—	—	—	0	—	0
Rough grassland	8 %	-	++	++	++	+	+	—	—	—	—
Grassland/Scrub	7 %	+	+	++	+	+	++	++	+	—	+
Rough vegetation	9 %	0	0	0	—	0	0	-	++	0	0
Scrub	41 %	-	—	—	—	-	—	0	-	—	—
Woodland	14 %	+	-	0	—	—	—	—	—	++	++

Table 2.2.4
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. Non-significant 3-way and 2-way interactions were eliminated from the final model.

		Grazing time			**Bites**			**Bite Rate**		
	df1	**df2**	**F**	**P**	**df2**	**F**	**P**	**df2**	**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*Season	3			n.s.			n.s.			n.s.
Species*Height	2	128	9.02	**<0.001**	128	10.37	**<0.001**			n.s.
Height*Season	6	124	5.62	**<0.001**	124	4.84	**<0.001**	71.3	4.59	**<0.001**
Species*Height *Season	6			n.s.			n.s.			n.s.

Table 2.2.5

Plant species from which more than 500 bites were taken during the 30 sessions of six hour periods for both cattle and ponies. Class: G: graminoids; F: forbs; W: woody plants. 'mix of graminoids' and 'mix of forbs' were 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.

Highland cattle			**Shetland ponies**		
Plant species	**Class**	**% Bites**	**Plant species**	**Class**	**% Bites**
mix of graminoids	G	79,31	mix of graminoids	G	4,36
Carex arenaria	G	2,83	*Carex arenaria*	G	5,78
Juncus subnodulosus	G	2,00	*Holcus lanatus*	G	3,94
Rubus caesius	F	1,83	*Claytonia perfoliata*	F	3,82
Holcus lanatus	G	1,60	*Scirpus setaceus*	G	3,22
Claytonia perfoliata	F	1,53	*Carex riparia*	G	1,30
Urtica dioica	F	1,51	*Agrostis stolonifera*	G	1,17
Salix repens	W	1,32	*Calamagrostis epigejos*	G	1,14
Rosa pimpinellifolia	W	0,91	*Juncus subnodulosus*	G	1,14
Calamagrostis epigejos	G	0,89	mix of forbs	F	0,66
mix of forbs	F	0,73	*Rubus caesius*	F	0,49
Carex riparia	G	0,72	*Poa trivialis*	G	0,48
Hippophae rhamnoides	W	0,62	*Stellaria media*	F	0,47
Prunus spinosa	W	0,62	*Urtica dioica*	F	0,25
Clematis vitalba	W	0,54			

Table 2.2.6

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

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 & 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

Table 2.2.7

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

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.

Habitat use overlap				
	Summer	**Autumn**	**Winter**	**Spring**
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				
	Summer	**Autumn**	**Winter**	**Spring**
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

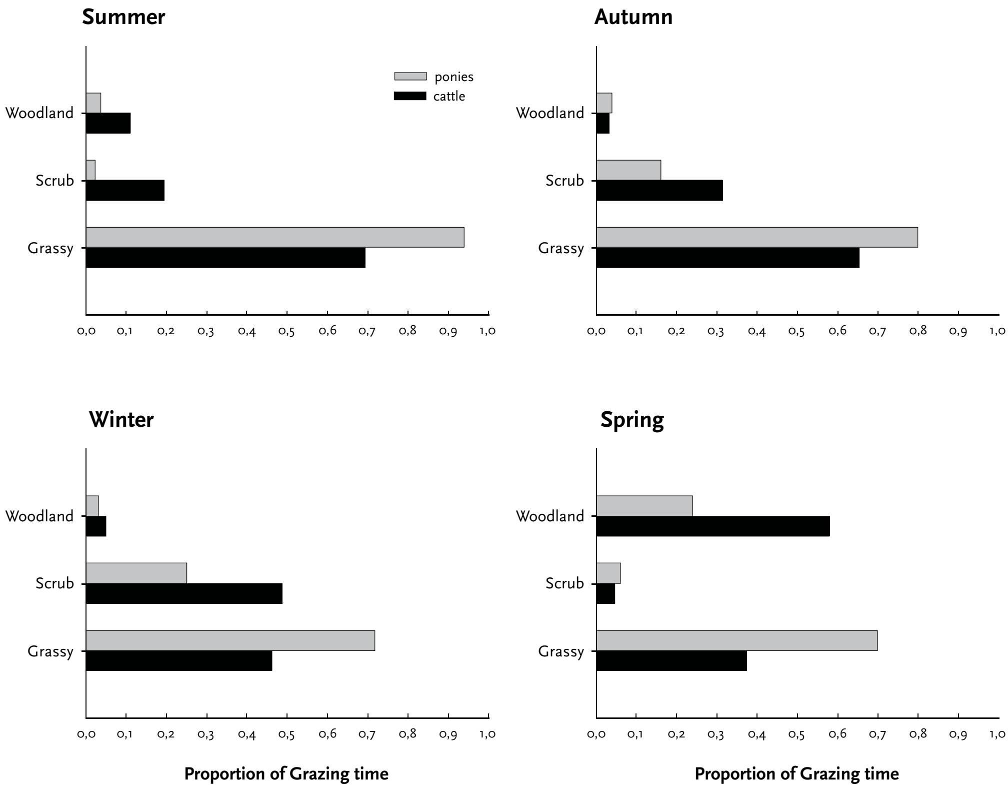


Figure 2.2.1
Habitat use of cattle and ponies in the different seasons: the proportion of grazing time spent in the three habitat types

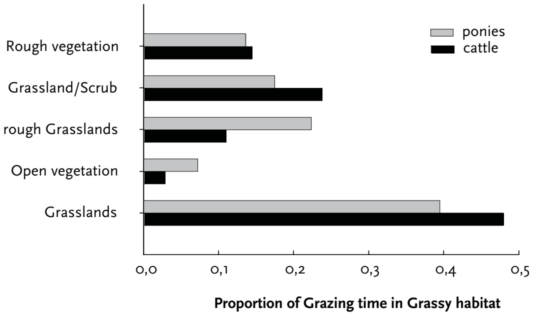


Figure 2.2.2
The proportion of grazing time spent in the five vegetation units within the habitat type 'grassy habitat', averaged over the four seasons

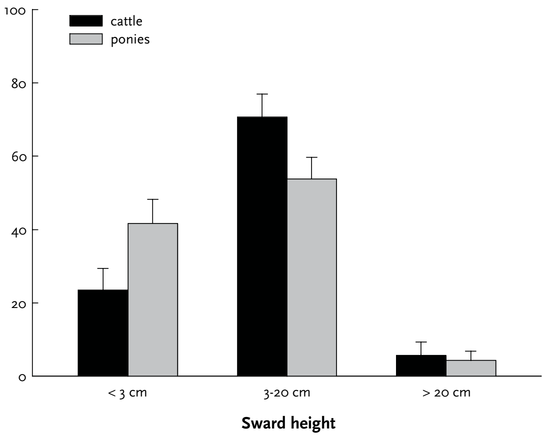


Figure 2.2.3
Proportion of the grazing time, when foraging in grasslands, spent in the different sward heights.

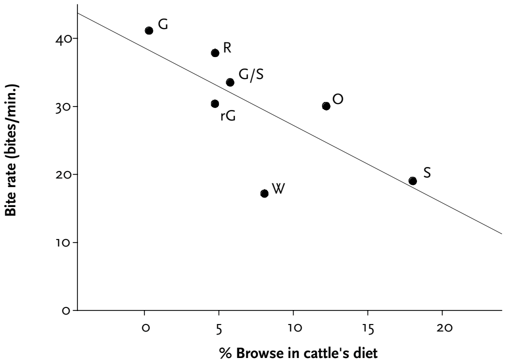
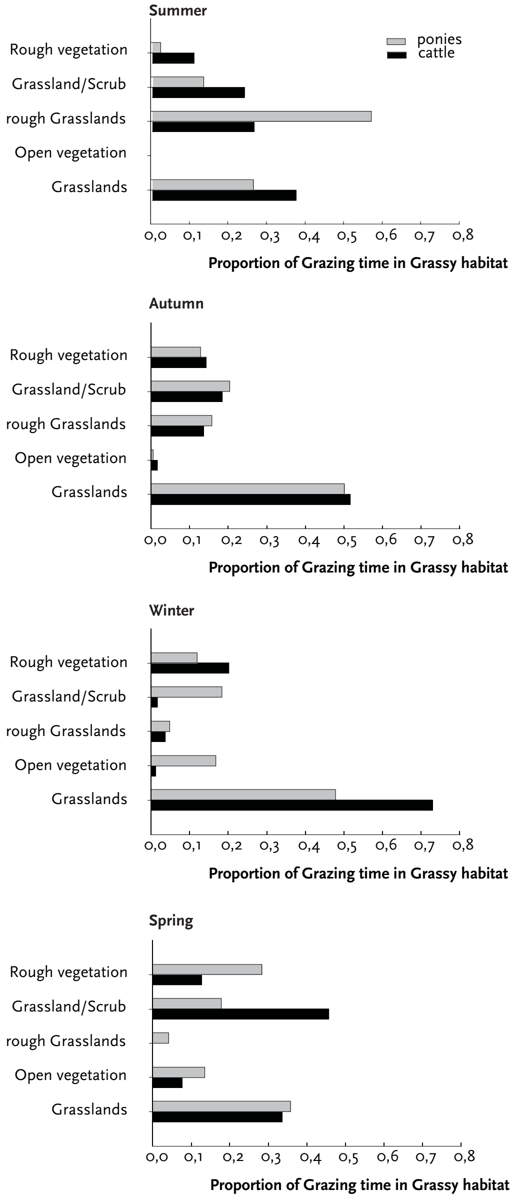


Figure 2.2.4
Relation between the percentage browse in the cattle's diet and the bite rate when foraging in the different habitat types. G: grasslands; rG: rough grasslands; R: rough vegetation; G/S: grasslands with scrub invasion; W: woodland; O: open vegetation and moss dunes; S: scrub



Addendum - Figure 2.2.5
The proportion of grazing time spent in the five vegetation units within the habitat type ‘grassy habitat’, in all four seasons.

2.3. Foraging behaviour of donkeys grazing in a coastal dune area in temperate climate conditions

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Donkeys, Houtsaegerduinen (foto: Indra Lamoot)

Abstract

A small herd of donkeys was introduced in a coastal dune reserve ‘Houtsaegerduinen’ (ca 80 ha) in Belgium, in order to slow down expansion of dominant grass and shrub species. The Houtsaegerduinen is a nutrient poor, scrub-dominated dune system with a spatially heterogeneous vegetation pattern. Different aspects of the grazing behaviour (grazing time, bite rate, habitat use, diet composition) of the free-ranging donkeys are described and analysed. Behavioural data (of max. six adult mares) were collected through continuous focal animal observation in three consecutive years (1998-2001). Temporal variation in grazing time, habitat use and diet composition was determined.

During daylight, donkeys spent most of their time on grazing (56%). In all three years, grazing time was significantly shorter in summer (45% of their time), longest grazing times were achieved in spring (64%). In spring, the donkeys also achieved the highest bite rate (21.5 bites/min). The grassy habitat was preferred for foraging in all seasons, while the use of scrub and woodland was variable over time. Averaged over the four seasons, the general diet consisted for 80% of graminoids, 10% of forbs and 10% of woody plants. However, diet composition varied not only among seasons and years, but depended also on the foraged habitat type. More time is needed to evaluate the impact of the donkeys on the vegetation, though some plant species seem to be hampered by the donkeys. *Calamagrostis epigejos*, vulnerable to grazing, is a main component of the donkeys’ diet. Grassland dominated by *C. epigejos* start to develop into less monospecific grasslands. *Ligustrum vulgare* is browsed intensively from autumn till spring and becomes less vital when growing in accessible places. Donkey grazing will not avoid further encroachment of *Hippophae rhamnoids*, since it is rarely consumed by the donkeys.

Keywords: grazing behaviour, habitat use, donkey, equid, diet composition

Introduction

Until the beginning of the twentieth century practically all coastal dunes in Belgium were grazed for agricultural purposes. After several decades of abandonment, a number of dune areas are grazed again, but now for reasons of nature management (Provoost et al. 2002). In the late 1990's different species of domesticated large herbivores were introduced in several dune reserves in order to avoid further expansion of dominant, highly competitive grass and shrub species. However, little knowledge was available on the ability of the herbivores to fulfil the management objectives as well as on the ability of the herbivores to cope with this low productive, scrub-dominated ecosystem. Therefore, it was decided to introduce different herbivore species in order to be able to evaluate which species can cope with this environment without problems, and secondly, which species can fulfil the management objectives best. Donkeys, Shetland ponies, Konik horses and Highland cattle were introduced in different dune areas.

The donkey is not the most commonly used herbivore species in nature reserves in West Europe. Nonetheless, the donkey was chosen as one of the herbivore species for several reasons. The feral donkey (*Equus asinus*) originates from an arid, low productive environment (Bauer et al., 1994) and was therefore assumed to be suitable to graze in a nutrient poor and dry dune ecosystem. Compared with other equids, donkeys are expected to cope more easily with adverse nutritive conditions due to a higher digestion efficiency (Izraely et al., 1989; Cuddeford et al. 1995). Additionally, it was expected that donkeys would browse more than other equids. Moehlman (1998a) reported that the donkey has the dentition for grazing, though it also appears to have special adaptations for browsing. The donkey has a very mobile upper lip and is able to curl it around the thorniest vegetation.

The general aim of the present study is to describe different aspects of the grazing behaviour (i.e. grazing time, number of bites, bite rate, meal duration) of donkeys, free-ranging in a temperate coastal dune area, in order to provide more understanding about their foraging strategy in such a relatively nutrient poor ecosystem. Since nutrient and energy restrictions are even more pronounced during the seasons with low plant productivity, we expected that the donkeys would adapt their foraging behaviour to these seasonal differences in forage quality and quantity. We also investigated whether the donkeys changed their grazing behaviour over a period of three years, from introduction onwards. Furthermore, our results about the donkeys' habitat use and diet selection are used to evaluate whether the introduction of donkeys is a good management measure to reach the nature conservation objectives.

Materials and Methods

Study site and animals

Five donkey mares and one donkey stallion (*Equus asinus*) were released in April 1997 in the coastal nature reserve "Houtsaegerduinen". One more mare was introduced in 1999 and eight foals were born since introduction, leading to a herd of seven adult mares, two two-year-old mares, two adult stallions, one two-year-old stallion and three colt foals of almost 1 year in spring 2001. The nature reserve (total area ca. 80 ha) is a nutrient poor (unpubl. data Cosyns) coastal dune system with a spatially heterogeneous vegetation pattern. It is located in a coastal region with mild winters and mild summers. Mean annual temperature is 9.8°C. In summer, autumn, winter and spring, mean temperature is 15.9°C, 10.8°C, 3.9°C and 8.7°C, respectively; mean monthly precipitation is 60.7mm, 74.8mm, 56.5mm and 48.5mm, respectively (means for the period 1963-2002; Meteo WVL vzw). Approximately two thirds of the area is covered by more or less closed scrub vegetation, main shrub species are *Hippophae rhamnoides, Ligustrum vulgare* and *Salix repens.* Woodland covers approx. 10% of the area. Tree species are *Populus tremula*, *Populus x canadensis*, *Populus canescens, Alnus glutinosa* and *Ulmus minor*. The remaining 23 % of the area is covered by patches of grassy vegetation. Within the latter habitat type, we distinguish the vegetation units 'grassland', 'rough grassland', 'grassland with scrub invasion', 'rough vegetation' and 'open vegetation and moss dune'. Grassland includes dry dune grassland with *Poa pratensis*, *Avenula pubescens, Veronica chamaedrys, Galium verum* and *Thalictrum minus* and grassland with *Holcus lanatus* and/or *Arrhenatherum elatius* as main graminoids. Rough grassland is defined as species-poor grassland dominated by

Calamagrostis epigejos. Grassland with shrub invasion consists of a grass-dominated matrix in which patches of young shrubs of mainly *Hippophae rhamnoides, Ligustrum vulgare* or *Salix repens* appear. Rough vegetation is the assembly of vegetation entities dominated by *Rosa pimpinellifolia* and vegetations characterized by tall forbs (e.g. *Eupatorium cannabinum*, *Urtica dioica, Cirsium arvense*). Mosses and lichens are the dominant species of moss dunes. Main species of open vegetation are *Carex arenaria*, *Festuca juncifolia* or *Ammophila arenaria*.

Mean weight of the adult mares was 175 ± 7 kg (weighed in May 2000, March and October 2001). The animals are free-ranging and remain in the area year round. They receive no additional food.

Behavioural observations

The grazing behaviour and habitat use of the donkeys was investigated discontinuously during a period of three years. Four observation periods can be distinguished (Table 2.3.1). Observation sessions were pre-scheduled on specific data. Consequently, weather conditions vary among observation sessions.

Data were collected through continuous focal animal observation (Altmann, 1974). During a six-hour period we continuously monitored the behaviour of one focal animal, except for period ‘2001’. Then, two focal animals were observed, each for three hours. The observed animals were habituated to the presence of humans and could be approached closely (1 m) without visible influence on their behaviour. Observational data are from five, six, two and four adult mares in 1998, 1999, 2000 and 2001, respectively. The duration (accuracy: 1 s) of the observed behaviours and the vegetation type in which the behaviour was performed were recorded. The different vegetation types were clustered 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. During the 2000 period, every 15 minutes the position of the focal animal was marked on a false colour infrared aerial photograph (1/2000) (EUROSENSE, flight date: 1998). During the 1999 and 2001 period, we additionally recorded

plant species eaten and the number of bites taken (using a mechanical counter), when the focal animal was grazing. All plant species eaten were grouped into four forage classes: 'graminoids' (grasses, sedges and rushes), 'forbs', 'woody plants' and 'other' (including mosses and ferns, unidentifiable plant material, soil).
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).

Data analysis

Grazing behaviour

In a first exploration of the data, we investigated whether the time spent grazing differed between nocturnal and daytime hours. During 1998, the observations (258 hrs) were conducted between 0h00 and 24h00, 58% of which were performed during daytime hours. In 1999 the observations (282 hrs) took place between 6h00 and 24h00, 75% of which were done during daytime. In 2000 all observations (198 hrs) were performed during daytime. Consequently, we only retained the data from 1998 and 1999 for this analysis. We used mixed-models ANOVA to investigate the effects of the fixed factors DayNight, Year and Season and all possible interactions on the differences in grazing time per hour. We included the factor Season and Year, because temporal differences in the grazing time could exist. In addition, differences in the grazing behaviour between individual animals could occur. Therefore, we initially included the random factor 'Individual' (and all interactions between 'Individual' and the fixed factors) in the ANOVA model. Since the individual animals were sampled more than once, we included the repeated statement in the statistical model. Covariance structure was calculated with the autoregressive method, because this always gave the best fitting model. 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 the ANOVA model. The random factor and the repeated statement were also implemented in all subsequent ANOVA models and will not be mentioned again.

All further analyses were based on the observations done during daytime. The time budget was calculated as the proportion of six hours spent on the behaviours ‘grazing’, ‘resting up’, ‘laying down’, ‘walking’, ‘standing alert’, ‘grooming’ and ‘other behaviour’. Other behaviour includes drinking, defecating, urinating, mutual grooming, rolling, sniffing and all interactive behaviour. We analysed whether the variable ‘grazing time’ was different among seasons and between years, by the use of a mixed-models ANOVA with the fixed effects Season and Year. In addition, we investigated the variable ‘meal duration’ during 2000. A meal is defined here as a period during which the animal is mainly grazing, including short interruptions (max. 5 minutes) of non-grazing activity, e.g. scanning of the environment. When the focal animal stops grazing for more than five minutes, the next observation of grazing is considered to be the start of a new meal. Although considered part of a meal, short interruptions are excluded from the calculation of the meal *duration*, in order to include only true grazing activity. Mixed-model ANOVA was used to investigate whether meal duration differed among seasons.

The positional data collected every 15 minutes during a six hour period in 2000, enabled us to estimate the cumulative distance travelled per observation session, assuming straight line displacement between two location recordings. We analysed whether this travel distance was different among seasons, using an ANOVA-model. In addition, the correlation between distance travelled per six hours and total grazing time per six hours was calculated (Spearman correlation, N = 32).

Habitat use

The habitat use was defined as the time spent grazing in the different habitat types. We investigated habitat use at two different levels: (1) the level of the habitat type, (2) the level of the vegetation unit within the grassy habitat. Thus, we first examined how the donkeys divided their grazing time over the grassy habitat, scrub and woodland. Subsequently, we studied the donkeys grazing time partitioning among grasslands, rough grasslands, grasslands with scrub invasion, open vegetation and rough vegetation, when they were foraging in the grassy habitat. The variation in grazing time was examined with a mixed-model ANOVA. Fixed factors were Habitat (or Vegetation unit), Season, Year and all their interactions.

In addition, we calculated the Jacobs' index of selection (1974) to describe the habitat preference, while taking into account the availability of the different habitat types. Jacobs' index of selection (1974): $D_i = (p_i - A_i)/((p_i + A_i) - (2^* p_i * A_i))$ with p_i the mean proportion of the 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 values indicating avoidance and selection of the habitat type, respectively.

Diet composition

We determined whether number of bites taken and bite rate (number of bites per grazing minute) differed among seasons using a mixed-model ANOVA with the fixed factor Season (data from 1999). Subsequently, diet composition and its temporal changes were examined. We analysed whether the factors Class, Season, Year and the interactions affected the proportion of bites per forage class (data from 1999 and 2001). Finally, we analysed whether the diet composition depended on the foraged habitat type. Therefore, we calculated the proportion of bites taken per forage class in a habitat type. Fixed factors of the ANOVA model are: Class, Habitat, Season, Year and all interactions.

Data which are proportions were arcsine 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 digitized and processed with ArcView GIS 3.2a.

Results

Daytime versus nighttime grazing

The factor 'DayNight' had a significant effect on the grazing time per hour ($F_{1,318} = 86.27$; $p<0.001$). During the nocturnal hours the donkeys grazed less than during the daytime hours, i.e. 22 min/hr during the night and 37 min/hr during the day. In addition, there was a Year-effect ($F_{1,167} = 6.68$; $p=0.011$) and a significant interaction DayNight*Year ($F_{1,309} = 5.00$, $p=0.026$). During nocturnal hours, the donkeys grazed longer per hour in 1998 than in 1999. The grazing time per hour (during the night and the day) was not significantly different among seasons. As a consequence of the significant differences in grazing time during day and night, all further analyses were based on daytime-data only.

Time budget during daytime

The time budget of the donkeys in the different seasons, averaged over the three years, is presented in Table 2.3.2. Grazing was pre-eminently the most time-consuming behaviour. Grazing time varied among seasons and years, since significant effects of Season ($F_{3,45.7} = 7.61$; $p < 0.001$) and of Year ($F_{2,29.2} = 7.50$; $p = 0.002$) were found. From 1998 towards 2000 the time spent on grazing steadily decreased (65.1 %, 60.7 % and 52.4% in 1998, 1999 and 2000, respectively). The reverse pattern was found for resting time (14.3%, 23.2% and 28.1% in 1998, 1999 and 2000, respectively). In all three years (no significant interaction Season*Year), the donkeys grazed significantly shorter in summer, while longest grazing times were achieved in spring. The opposite trend was found for the time spent resting: longest resting times in summer, shortest in spring. The time investment in the other behaviours remained relatively constant over the different seasons (see Table 2.3.2).

Meal duration (period 2000) averaged 32.4 ± 3.1 min. Although mean meal duration in summer, autumn, winter and spring appeared quite different (19.3 ± 3.3 min, 38.0 ± 8.3 min, 33.0 ± 6.0 min and 40.2 ± 6.3 min, respectively), ANOVA results showed that these seasonal differences were not significant.

Mean travel distance per 6 hours was 917m ± 138m. It was not significantly different among seasons. Travel distance per 6 hrs was positively correlated with grazing time per 6 hrs ($r = 0.536$; $p = 0.002$; $N = 32$).

General habitat use

ANOVA analysis clearly shows the habitat use variation among seasons and among years (see Figure 2.3.1), since significant interactions Habitat*Season ($F_{6,180} = 2.69$; $p = 0.016$) and Habitat*Year ($F_{4,180} = 10.28$; $p < 0.001$) occur. The significant 3-way interaction ($F_{12,180} = 1.94$; $p = 0.032$) shows that the seasonal variation in habitat use was not similar over the three years. The significant factor Habitat ($F_{2,180} = 102.06$; $p < 0.001$) illustrates that the donkeys did not divide their grazing time uniformly over the three habitat types, irrespective of the season or the year. The grassy habitat was the most grazed habitat in all seasons and in all three years. The use of scrub and woodland was variable among seasons and between years. In general, the donkeys foraged most in scrub and woodland in autumn and winter. The use of woodland decreased steadily from 1998 to 2000 (73, 26 and 7min/6hrs in the winter of 1998, 1999 and 2000, respectively). Instead, the use of scrub increased from 1998 to 2000 (27, 57 and 95min/6hrs in the winter of 1998, 1999 and 2000, respectively). From the Jacobs' index for selection it can be concluded that woodland evolved from a slightly preferred habitat in 1998, via 'neutral' habitat in 1999 towards strongly 'avoided' habitat in 2000 (Table 2.3.3). Although scrub was grazed very intensively in autumn and winter 2000, we could not conclude that it was ever a 'preferred' habitat. This is probably caused by the dominance of scrub in the area (i.e. 67 % of the area).

Habitat use differentiation within grassy habitat

When comparing the grazing time spent in the vegetation units distinguished within the grassy habitat (periods 1998 and 2000), we found the significant interactions Vegetation*Season ($F_{12,210} = 1.86$; $p = 0.041$), Vegetation*Year ($F_{4,210} = 7.58$; $p < 0.001$) and Vegetation*Season*Year ($F_{12,210} = 2.54$; $p = 0.004$). Hence, the use of the vegetation units within the grassy habitat is different among seasons and between years. The significant 3-way interaction shows that the seasonal variation is different between both observation periods. Without taking into account the seasonal variation, we can conclude that the donkeys spent more grazing time in the open vegetations and grasslands, in 1998 than in 2000. On the other hand, the donkeys spent more grazing time in rough vegetation in 2000 (Figure 2.3.2).

Number of bites per season and diet composition

The number of bites taken per day (in 1999) was significantly affected by the factor Season ($F_{3,17.4} = 4.39$; $p = 0.018$). The donkeys took significantly more bites in spring than in all other seasons (2006 ± 394 bites/6h, 2604 ± 364/6h, 2874 ± 590/6h and 5273 ± 701/6h in summer, winter, autumn and spring, respectively). This was not only the result of a longer grazing time in spring, but also of an increased bite rate in spring compared to the other seasons (10.5 ± 0.4, 11.6 ± 0.9, 13.6 ± 1.8 and 21.5 ± 1.6 bites/min grazing in summer, autumn, winter and spring, respectively). The factor Season had indeed a significant effect on the variable bite rate ($F_{3,17.8} = 5.03$; $p = 0.011$).

The total diet of the donkeys consisted of 19-26 species of graminoids, 38-48 species of forbs and 24-22 woody plant species (1999 versus 2001). In Table 2.3.4 the most frequently bitten plant species (>500 bites taken during 132 and 219 observation hours in 1999 and 2001, respectively) are given. It is obvious that graminoids were of major importance in the diet. Throughout the year, in both observation periods (1999, 2001), diet consisted for 80 % of graminoids, 10-11% of forbs and 9-10% of woody plants. However, the diet composition was variable among seasons (Figure 2.3.3). The proportion of bites taken per forage class was significantly affected by the interactions Class*Season*Year ($F_{6,257} = 7.60$; $p < 0.001$) and Class*Season ($F_{6,259} = 5.10$; $p < 0.001$) and the factor Class ($F_{2,259} = 337.30$; $p < 0.001$), indicating that seasonal differences in diet composition were not similar in both years. For example, the biggest proportion of woody plants and forbs in the donkeys' diet in 1999 was found in summer, while in 2001 this was found in winter. A remarkable aspect is that in summer 1999 the donkeys took a similar number of bites of woody plants and graminoids, but this is entirely caused by the consumption of *Rosa pimpinellifolia* fruits (classified as woody plant) in summer. The donkeys took even more bites of *Rosa pimpinellifolia* than of *Calamagrostis epigejos* in summer 1999, while in the other seasons, in the absence of rose hips, *Rosa pimpinellifolia* was bitten only rarely. In 2001, *Rosa pimpinellifolia* hips were far less frequently consumed (see Table 2.3.4).

Diet composition depended on the foraged habitat type and this varied as well among seasons and between years (Table 2.3.5). Averaged over the four seasons, the proportion of graminoids in the diet is highest when the donkeys grazed in the grassy habitat, in both 1999 and 2001. When foraging in scrub, the relative proportion of graminoids decreased mostly in favour of forbs in 1999, while mostly in favour of woody plants in 2001. When foraging in woodland, the relative proportion of graminoids decreased in both years in favour of forbs. The contribution of woody plants to the diet, when foraging in woodland, was only slightly higher than when foraging in grassy habitat. However, browsing activity in woodland depended strongly on season and year. For example, in autumn 1999 and in spring 2001 the donkeys browsed much more when foraging in woodland than in the grassy habitat. According to the ANOVA analysis, diet composition is significantly affected by the foraged habitat type (significant Class*Habitat: $F_{4,471} = 14.39$; $p < 0.001$). However, this result can not be interpreted without attention for the significant interactions Class*Habitat*Season ($F_{12,485} = 5.14$; $p < 0.001$) and Class*Habitat*Year ($F_{4,470} = 8.37$; $p < 0.001$), which illustrate that the variation in diet composition per habitat type was different among seasons and between years. Other significant effects on the proportion of bites are: Class*Season*Year, Class*Year, Class*Season and Class.

Discussion

Little knowledge is available on the grazing behaviour of donkeys (Aganga & Tsopito, 1998; Canacoo & Avornyo, 1998; Moehlman, 1998a, 1998b), certainly in cool temperate regions, where they experience significantly different environmental conditions than in their environment of origin. As all free-ranging herbivores, donkeys have 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 & Gordon 1993). The foraging decisions are primarily made in relation to forage availability and quality, which are in turn determined by environmental conditions. Different aspects of the foraging behaviour are treated here consecutively.

Some studies have reported on remarkable physiological differences between the donkey and other equids. In particular, several studies reported on the donkeys' capacity to deal with dehydration (Izraely et al., 1994) and with their higher digestive efficiency compared to other equids (Izraely et al., 1989; Cuddeford et al., 1995; Pearson et al., 2001). Izraely et al. (1989) found that the digestive efficiency of donkeys is as high as that of Bedouin goats, with the latter being more efficient than non-desert ruminants. The capacity of donkeys to digest plant cell wall constituents is lower than that of Bedouin goats and other ruminants but higher than that of ponies or horses. The donkey reaches the same digestive efficiency as the Bedouin goat as a result of its higher intake rate and higher efficiency to absorb soluble cell content components. Cuddeford et al. (1995) compared the digestive efficiency among Thoroughbreds, Highland ponies, Shetland ponies and donkeys. Donkeys retained food longer in the digestive tract and digested fibre more efficiently than did the other equids. In that sense, donkeys were more 'ruminant-like'. This was confirmed by Pearson et al. (2001): donkeys had longer retention times and a higher digestibility of dry matter, energy, crude protein and fibre fractions than ponies. They also found that donkeys consumed less dry matter per unit metabolic body weight when fed ad libitum than ponies. Since voluntary food consumption is proportional to metabolic rate (Kleiber, 1961; Webster, 1985), this may illustrate that donkeys have a lower metabolic rate, and hence lower maintenance requirements than the ponies. These differences in requirements and digestive abilities between donkeys and other equid species can lead to differences in their foraging behaviour in a free-ranging situation.

Time budget

Quite similarly to other equids (Duncan, 1985; Pratt et al., 1986; Berger et al. 1999), the donkeys grazed longer during daytime hours than during nocturnal hours.

Spending on average 56 % of the daytime on grazing and 22 % on resting, donkeys are average equids compared to free-ranging or feral horses. Duncan (1985) reported that Camargue horses generally spend 50-70% of a whole day on feeding and 20-30% on resting. Przewalski horses in a nature reserve in the Mongolian steppes on average only grazed 49% of the daytime (van Dierendonck et al., 1996). In a study in Ghana, donkeys spent 84% of their time grazing during the day (at night they were sheltered in pens). The authors suggested that this prolonged grazing could be in part the result of the poor quality of the pasture that the donkeys were grazing (Canacoo and Avornyo, 1998). Female feral donkeys in the dry habitat of Death Valley (US) and in the mesic habitat of Ossabaw Island (US) grazed for 52.8% and for 41.6 % of their daytime, respectively (Moehlman, 1998b). In environmentally more comparable situations (neighbouring coastal dune areas) the donkeys in the present study spent less time on grazing than other free-ranging equids. Haflinger horses spent 68% of the daytime on foraging (Lamoot & Hoffmann, 2004), while Shetland ponies grazed 71% of their daytime (Lamoot et al., in press) and Konik horses spend 73 % of the period between 6h and 24h on grazing (Cosyns et al., 2001). The higher digestive efficiency of the donkeys compared to other equids (Izraely et al., 1989; Cuddeford et al., 1995; Pearson et al., 2001) probably gives them advantage when feeding on the relatively low quality food in a dune ecosystem, resulting in a smaller time investment in grazing.

In a period of three years we found a trend of decreasing grazing time. The herd enlarged from the start of the observation period towards the end, implying possible increase of interactive behaviour. The time spent on 'other behaviour', including interactive behaviour; raised from 3 min/6 hrs in 1998 up to 10 min/6 hrs in 2000. However, this remains a low time investment and can not be responsible for the much larger decrease in grazing time. Resting time on the other hand, is a relatively high time investment behaviour; it doubled from 1998 to 2000. This underpins the suggestion that the donkeys developed a more efficient foraging strategy. We assume that the extended knowledge of the environment, especially on nutritional quality and quantity, diminished the need for foraging time investment allowing for more resting time. It has been reported that naive animals spend more time foraging but ingest less forage compared to experienced animals (Provenza & Balph, 1987, 1988). Our data suggest that this phenomenon appears even more strongly so in a complex, heterogeneous environment.

Grazing time increased from summer, over autumn and winter towards spring. An increased grazing activity of equids in winter compared to summer has been reported several times for the temperate regions (Duncan, 1985; Duncan, 1992; Pratt et al., 1986; Berger et al., 1999; Cosyns et al., 2001; Menard et al., 2002), as well as in subarctic conditions (Salter & Hudson, 1979). Those authors investigating foraging behaviour in spring as well, found foraging times in spring comparable to those in winter (Duncan, 1985; Duncan, 1992) or reported higher grazing times in spring than in winter (Pratt et al., 1986; Berger et al., 1999). It is generally accepted that seasonal variation in grazing time is mainly caused by seasonal variation in forage quantity and quality, e.g. Duncan (1985) suggested that the horses in the Camargue increased their feeding time in winter in an attempt to maintain a high quality diet. Pratt et al. (1986) put forward that the peak in the ponies' feeding activity in the months of April and May in the New Forest is the result of the exploitation of the new grazing resources. A limited number of biomass data of Houtsaegerduinen (unpubl. data, Cosyns) supports a causal relation between grazing time and general food availability. The average graminoid standing crop in the grassy vegetation units differed among seasons, i.e. 327, 205, 196 and 177g/m? in summer, autumn, winter and spring, respectively. Live biomass covers 80%, 79%, 49% and 72% of this graminoid standing crop in summer, autumn, winter and spring, respectively. Hence, graminoid quantity decreases from summer, over autumn and winter to a minimum in spring, and the quality of the graminoid standing crop decreases from summer to winter and starts to increase again in spring. An increased grazing investment can thus be related to a decreased quantity and quality of graminoids. We suggest that the long grazing time in spring, accompanied with a higher bite rate compared to the other seasons, is the result of the general low food quantity combined with the new availability of better quality food provided by the fresh regrowth of graminoids with the start of the growing season.

Habitat use

In quite different ecosystems all over Europe it was found that equids show a strong preference for grassland (Camargue: Duncan 1983; Menard et al. 2002; New Forest: Pratt et al. 1986; Putman et al. 1987; Rhum: Gordon 1989a). The donkeys in the present study are no exceptions to that rule. Throughout the year, the grassy habitat was preferred by the donkeys, although, habitat use was influenced by seasonal characteristics. In all three years, grazing time was almost entirely restricted to grassy habitat in summer and spring (with the exception of spring in period 1998), while in autumn and winter, a certain shift towards woodland and scrub was observed. Remarkable is the increasing foraging activity in scrub during the later autumn and winter periods. Shetland ponies and Haflinger horses living in neighbouring dune areas both preferably grazed in graminoid-dominated vegetations as well. However, Haflinger horses did not perform a higher foraging activity in scrub or woodland during autumn and winter (Lamoot & Hoffmann, 2004). Shetland ponies increased the use of scrub in autumn and winter, while the use of woodland increased in spring. In these habitat types they remained on a diet of graminoids and forbs, and did not browse (Lamoot et al., in press).

The increased use of scrub and woodland during autumn and winter coincides with a general decline in (live) biomass of the grassy vegetation units (unpubl. data Cosyns; see above). The lower plant productivity of the grassy vegetations during the non-growing seasons is the most probable reason for the observed shift in habitat use (Duncan 1983; Gordon 1989b; Gordon & Illius 1989). The return to grassy habitat already in spring, when biomass is still very low, but new shoots deliver high quality food, indicates the animals strong preference for high quality food after a long period of its non-availability.

The use of woodland remarkably decreased during the observation period. This might be due to the decreasing availability of herbaceous undergrowth

over the years, which is the main diet in that habitat.
Changes in grass cover in rough grassland (certainly a grassland type with high biomass; unpubl. data Cosyns) after three years of donkey grazing probably affect the foraging behaviour of the donkeys. Permanent quadrates in grazed plots and ungrazed control plots in rough grassland (i.e. *Calamagrostis epigejos* dominated grassland) revealed a significant decline of *Calamagrostis* cover from an average of 63% towards 30% in the grazed plots between 1998 and 2001, while cover in the ungrazed control plots significantly increased (Vervaet, 2002). This definitely indicates that grass biomass availability declined severely in this relatively productive grassy habitat. Since *Calamagrostis epigejos* is an important component of the donkeys' diet, its decreased abundance may affect the foraging behaviour of the donkeys, forcing the animals to search for food in other vegetation types. The increased use of rough vegetation in 2000 compared to 1998 can be a result of this. The decreased availability of *C. epigejos* may also have an affect on the increased use of scrub from 1998 towards 2000. As *C. epigejos* is still an important forage in autumn, it can explain at least partly the increased use of scrub in autumn 2000 (37% of the grazing time). However, it cannot explain the intensive use of scrub in the winter of period 2000 (49% of the grazing time), since *C. epigejos* is much less grazed in winter.

Also at the more detailed scale of the grassy vegetation units, the donkeys' habitat use is variable over time, not only among seasons but also on the longer time scale. Habitat use flexibility is most probably the donkeys' answer to the temporal variation of the availability of food in the different habitats. Owen-Smith (1994) found that foraging behaviour of kudus was very elastic too. A changing habitat use expresses flexibility of the grazers, which is necessary to survive in a changing environment. We already suggested before that the donkeys became more efficient through the years. Habitat use is an outcome of the foraging strategy of the herbivores. The variation in habitat use between years may be a part of this developing foraging efficiency.

General diet composition

Horses are considered as true grazers that feed predominantly on grasses (Van Dyne et al., 1980; Putman et al., 1987; Duncan, 1992; Vulink, 2001). This is also the case for donkeys. Moehlman (1998b) reported that feral donkeys adapt their foraging behaviour to their environment: in Death Valley, an arid habitat, the donkeys are browsers and in the more humid habitat of Ossabaw Island the donkeys are grazers. Domesticated donkeys in Botswana are good grazers as well as browsers. During the dry season, when quality and quantity of the grasses is poor, the donkeys browse more (Aganga & Tsopito, 1998). Our data of 2001 showed a similar trend in the "Houtsaegerduinen", with an increased browsing activity in autumn and winter. In 1999 the donkeys browsed most in summer when they foraged selectively on hips of *Rosa pimpinellifolia*, though it is questionable whether this consumption of hips can be considered as a true browsing activity. Throughout the year the contribution of browse to the diet remained small though, certainly when compared to the contribution of graminoids (graminoids: 80%, forbs: 10-11%, woody plants: 9-10%).
Compared to Konik horses and Shetland ponies, which graze in nearby dune areas, the donkeys browsed a lot. The Konik diet contained no more than 2% browse (Cosyns et al. 2001). The ponies' diet consisted of 92% graminoids and 8% forbs, while they hardly consumed woody plants. In fact, diet composition of the donkeys showed more similarities with the diet of Highland cattle (graminoids: 87%, forbs: 8%, woody plants: 5%), grazing together with the ponies in the same dune area (Lamoot et al., in press). Woody plants have a high proportion of cell contents but poorly digestible cell walls, due to a high level of lignin, compared to graminoids (Illius & Gordon, 1993). Hindgut fermenters, like equids, are able to utilize the soluble components of the cell more efficiently than ruminants, but ruminants benefit from a greater efficiency in the extraction of energy from the cell wall (Rittenhouse, 1986). However, donkeys are far more efficient in digesting cell wall constituents than horses or ponies (Izraely et al., 1989; Cuddeford et al., 1995). Our results suggest that donkeys indeed browse more than other equids when foraging in a similar ecosystem.

Diet differentiation between habitats, seasons and years

Diet composition depended on the foraged habitat type, varied among seasons and changed over the years. Averaged over the four seasons, the donkeys consumed 82-85% graminoids when grazing in grassy habitat. When grazing in woodland the amount of graminoids in the diet decreased to 45-67%. In woodland the donkeys foraged a lot on undergrowth forbs (23-45%). In autumn and winter a considerable number of bites was taken from dead *Urtica dioica*, locally very abundant in the woodland undergrowth. In Botswana the donkeys peeled the bark of trees when there was food scarcity (Aganga & Tsopito, 1998). In the present study we have noticed that the bark of *Populus* trees in a horizontal position (cut down) was peeled off too. However, living trees of the same species in an upright position at the same spot were not harmed. Some other tree species were on the donkey's menu as well. They consumed leaves and branches of *Acer pseudoplatanus, Fraxinus excelsior, Populus alba, Ulmus minor, Alnus glutinosa* and *Prunus serotina*.

When foraging in scrub, the donkeys again mainly consumed graminoids (63-67%), they increased the contribution of forbs (12-19%), but they also showed a significant browsing activity (14-25%). *Ligustrum vulgare* is an important component of the donkeys' diet. Other browsed shrub species are: several *Rosa* species (mostly hips) and the exotic *Syringa vulgaris*. Furthermore, the donkeys browsed also on climbing plant species, such as *Clematis vitalba, Bryonia dioica* and *Hedera helix*.

In 1999, *Calamagrostis epigejos* was the main component of the donkeys' diet. The decreased abundance of *C. epigejos* in the grasslands dominated by this species in 2001, compared to 1998 (Vervaet, 2002; see above), probably influenced the diet composition of the donkeys in 2001. Besides an increased consumption of 'mix of graminoids', we found a doubled consumption of *Festuca juncifolia, Ligustrum vulgare, Rubus caesius* and *Urtica dioica* in 2001 compared to 1999.

A role in nature management?

Grazing management has been implemented in the "Houtsaegerduinen" to prevent the expansion of dominant grass species like *Calamagrostis epigejos* and *Arrhenatherum elatius* and the expansion of dense scrubs of *Hippophae rhamnoides* and *Ligustrum vulgare*, in order to maintain, extend or enrich dune specific grasslands (Provoost et al. 2002). Next to direct consumption of the dominant competitors, leading to a decrease of their abundance, the donkeys are expected to create structural diversity within monotonous vegetation types, dominated by the above-mentioned competitors.

Throughout the year, the donkeys spent most of their grazing time in the grassy vegetations. In addition, *Calamagrostis epigejos* is the main graminoid species of their diet (32% in 1999; 19% in 2001) (Table 2.3.4). From 1998 to 2001, grazed permanent plots in grasslands dominated by *C. epigejos* showed a significant decrease of the cover by *C. epigejos* and a significant increase in number of plant species. On the other hand, ungrazed control plots showed a significant increase of the cover by *C. epigejos* without a significant change in number of plant species (Vervaet, 2002). Thus, the donkeys seem to be suitable to avoid further dominance of *C. epigejos* in the rough grasslands, inducing even a certain species enrichment of these grasslands. Changes in the species composition of other grassland types, e.g. the species-rich dune grasslands, attributable to the grazing management, is not detected yet (unpubl. data Provoost). Similarly, more time is needed to evaluate the impact of the donkeys on scrubs. Probably, the impact of donkeys on the scrub will be smaller than on the grassy habitat, because they forage less in scrub. Nonetheless, they do forage and browse in scrub and open the scrub layer at least locally. A network of paths has been formed in the scrub habitat. *Ligustrum vulgare*, which is browsed intensively from autumn till spring, becomes visibly less vital when growing in accessible places, e.g. at scrub edges. *Hippophae rhamnoides*, which is considered as a problematic invasive shrub species, is rarely consumed by donkeys (fruits). Hence, herbivore introduction as sole measure will not suffice to avoid further encroachment of *Hippophae rhamnoides.*

Since the herd is still enlarging, it may be expected that the higher animal density will have a higher impact on the vegetation. Initially, one reason to choose donkeys as a grazing measure was the expectation that they would browse more than other equids. Although more experimental research is needed to compare feeding habits of donkeys with those of other equids, our data from neighbouring coastal dune areas with different equids, at least suggest that donkeys indeed browse more than ponies or horses. Their browsing activity appeared much more comparable to the browsing activity of cattle than that of other equids (Lamoot et al., in press). Another question related to the introduction of the donkeys as a management tool is whether they are able to cope with such a nutrient poor system. The donkeys in "Houtsaegerduinen" spent less time grazing and more time resting compared to other equids in similar systems. Body condition scores were determined a few times in 1999 according to the Condition scoring method for donkeys provided by McCarthy (1998). It was concluded that the donkeys were in good condition, i.e. not too skinny and not too fat, without a remarkable lost of condition during the winter period (unpubl. data Cosyns). Mean weight data of 5 adult mares was 180±8 kg on 04/05/2000, 166±15 kg on 21/03/2001 and 179±23 kg on 23/10/2001, respectively. Unfortunately, we do not have weight data from the summer period and from the end of the winter period, but the three measures do not show strong fluctuations, illustrating a rather stabile condition. The analyses of the blood samples, taken yearly from all the individuals, demonstrated that the donkeys did not show any deficiencies. We therefore conclude that the donkeys do not have problems surviving well in this particular ecosystem and that they probably can survive in conditions with even harder nutritional stress. Nowadays the domesticated donkey is no longer an important source of power in Western European countries, but it might play a role in nature management, especially in ecosystems providing only low forage quality.

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Table 2.3.1
Characteristics of the four observation periods. In the text we refer to the codes, instead of the observation periods.

Observation Period	Code	# sess. /month	N	Sampling session	Diurnal coverage	Observations
Aug'98 - May'99	1998	4	43	6 h	Day + Night (0-24h)	Behaviour, habitat use
Aug'99 - May'00	1999	4	47	6 h	Day + Night (6-24h)	Behaviour, habitat use, diet
May'00 - Apr'01	2000	3	33	6 h	Day	Behaviour, habitat use, location
Aug'00 - Jul'01	2001	3	37	2 x 3 h	Day	Behaviour, habitat use, diet

Table 2.3.2
Diurnal time budget of the donkeys, averaged over the three years. Mean and Standard error as percentages of a six hour period.

	Year		Summer		Autumn		Winter		Spring	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Grazing	56,2	3,1	45,4	4,0	57,6	2,4	57,8	2,6	63,9	3,3
Resting Up	17,7	2,8	20,2	3,4	14,7	2,4	21,0	2,5	14,9	2,9
Walking	8,9	0,8	8,4	0,8	10,2	0,8	10,1	1,0	7,1	0,7
Lying Down	4,6	1,4	8,4	2,3	4,5	1,2	1,4	0,6	4,2	1,5
Standing Alert	6,6	1,4	9,9	1,6	7,5	1,4	5,7	1,8	3,2	0,5
Grooming	4,0	0,7	4,6	1,1	4,0	0,6	2,3	0,4	4,9	0,8
Other behaviour	2,0	0,3	2,9	0,5	1,5	0,2	1,7	0,3	1,7	0,3

Table 2.3.3

Jacobs' index of selection (1974).

No selection (0): -0.08 < Index < 0.08. Avoidance (-): -0.4 < index < -0.08. Strong avoidance (—): index < -0.4. Preference (+): 0.08 < index < 0.4. Strong preference (++): index > 0.4

Habitat type	Area	1998	1999	2000
Grassy habitat	23,3 %	++	++	++
Scrub	67,0 %	—	—	—
Woodland	9,7 %	+	0	—

Table 2.3.4

Plant species from which more than 500 bites were taken during 132 hours in 1999 and during 219 hours in 2001. Class: G: graminoids; F: Forbs; W: Woody plants. 'mix of graminoids' was used to register a bite which contained several graminoids species, difficult to identify on the species level. This overview represents 93% and 92% of the total number of bites taken during observations in 1999 and 2001 respectively.

1999			2001		
Plant species	Class	% Bites	Plant species	Class	% Bites
Calamagrostis epigejos	G	31,62	mix of graminoids	G	21,35
mix of graminoids	G	16,43	*Calamagrostis epigejos*	G	19,15
Arrhenatherum elatius	G	12,28	*Festuca juncifolia*	G	14,83
Festuca juncifolia	G	8,13	*Arrhenatherum elatius*	G	10,36
Carex arenaria	G	7,50	*Carex arenaria*	G	5,54
Rosa pimpinellifolia	W	3,18	*Ligustrum vulgare*	W	3,69
Claytonia perfoliata	F	2,98	*Rubus caesius*	F	3,30
Elymus repens	G	2,04	*Urtica dioica*	F	3,28
Rubus caesius	F	1,78	*Holcus lanatus*	G	2,14
Ligustrum vulgare	W	1,72	*Clematis vitalba*	W	1,64
Urtica dioica	F	1,61	*Galium aparine*	F	1,62
Ammophila arenaria	G	1,39	*Hieracium umbellatum*	F	1,32
Poa trivialis	G	1,20	*Poa spec.*	G	0,86
Rosa canina	W	0,80	*Populus alba (+ P. x canescens)*	W	0,85
Festuca rubra	G	0,73	*Avenula pubescens*	G	0,72
			Rosa pimpinellifolia	W	0,72
			Ammophila arenaria	G	0,70

Table 2.3.5

Diet composition of the donkeys when foraging in grassy habitat, scrub and woodland, in the various seasons and throughout the year in 1999 and 2001. Bites per 6 (or 3) hrs: mean number of bites taken during a 6 (or 3) hour observation session in each of the three habitat types. %G: proportion of bites taken from graminoids. %F: proportion of bites taken from forbs. %W: proportion of bites taken from woody plants.

		1999				2001			
Season	**Habitat**	**Bites/6hr**	**%G**	**%F**	**%W**	**Bites/3hr**	**%G**	**%F**	**%W**
Summer	grassy	1619	44	15	41	822	87	10	3
	scrub	451	38	30	32	109	95	4	1
	woodland	131	30	67	3	86	81	9	10
Autumn	grassy	1840	84	8	8	788	80	13	7
	scrub	595	84	5	10	231	64	12	23
	woodland	297	62	15	23	187	33	59	8
Winter	grassy	1844	92	6	2	739	74	15	11
	scrub	810	87	8	5	293	56	19	26
	woodland	387	65	34	1	105	23	73	4
Spring	grassy	4592	92	7	2	1231	93	2	5
	scrub	587	43	39	18	98	42	2	56
	woodland	411	84	6	10	73	63	13	24
Year	grassy	2474	82	8	10	895	85	9	6
	scrub	611	67	19	14	183	63	12	25
	woodland	306	67	23	10	113	45	45	10

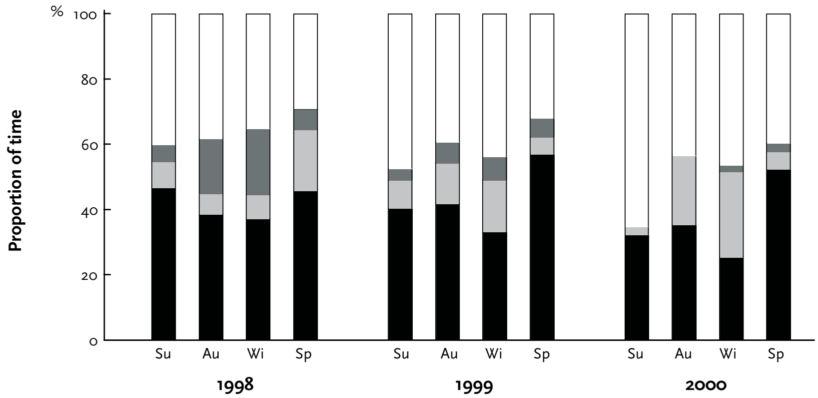

Figure 2.3.1

Habitat use of the donkeys, with its seasonal variation, in the three consecutive years.

Black represents the proportion of time spent grazing in the grassy habitat. Light grey: proportion of time spent grazing in scrub. Dark grey: proportion of time spent grazing in woodland. White: proportion of time spent to non-grazing activities. Su: summer, Au: autumn, Wi: winter, Sp: spring

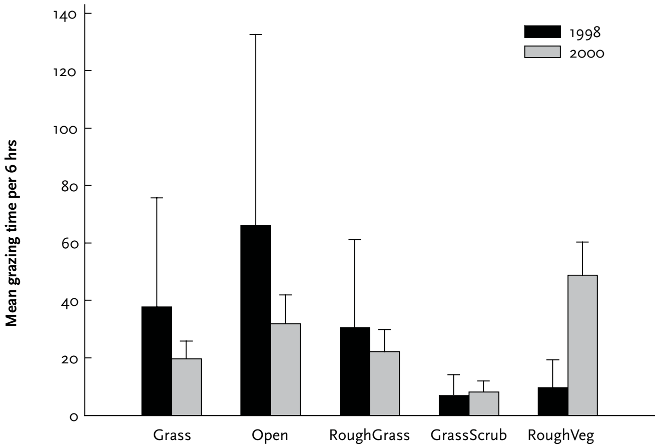

Figure 2.3.2
The use of the grassy habitat in 1998 and 2000. Mean grazing time ± SE per 6 hrs (min.) in the five vegetation types distinguished within the grassy habitat. Grass: grassland; Open: open vegetation and moss dunes; RoughGrass: rough grassland; GrassScrub: grassland with scrub invasion; RoughVeg: rough vegetation

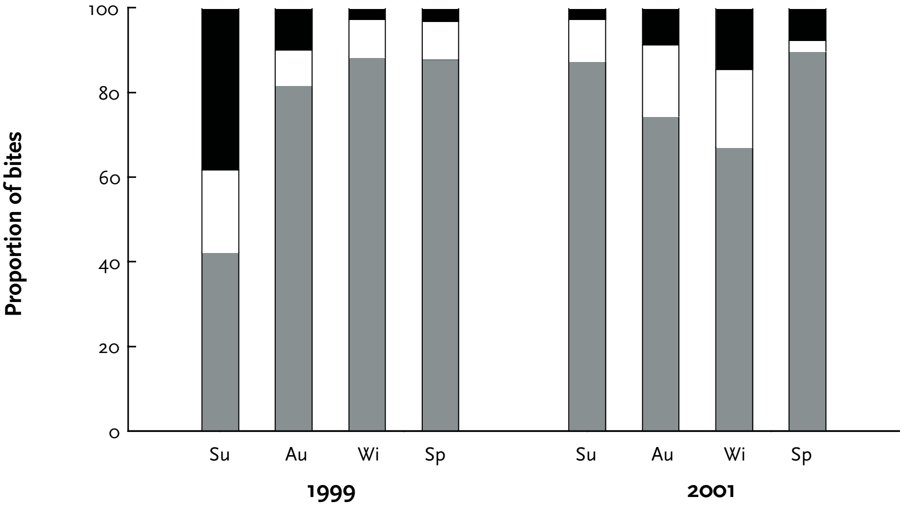

Figure 2.3.3
The donkeys' diet composition, with its seasonal variation, in 1999 and 2001. Grey: proportion of bites taken of graminoids; White: proportion of bites taken of forbs; Black: proportion of bites taken of woody plants. Su: summer, Au: autumn, Wi: winter, Sp: spring

3

GRAZING BEHAVIOUR OF FREE-RANGING DONKEYS AND SHETLAND PONIES IN DIFFERENT REPRODUCITVE STATES

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DONKEY MARE WITH FOAL, HOUTSAEGERDUINEN (FOTO: INDRA LAMOOT)

Abstract

We investigated how free-ranging mares of two species of equids (donkeys and Shetland ponies) modify their foraging behaviour to meet the increased nutritional requirements induced by lactation. We initially hypothesized that lactating mares would graze for a longer time and/or graze faster than non-lactating (dry) mares. The grazing behaviour of free-ranging animals, foraging in two low productive dune areas, was recorded during one year. Results show that in both species lactating animals did not spend more time grazing than non-lactating mares. However, lactating animals achieved a higher bite rate and, therefore took more bites than dry mares. Several factors affected the differences between lactating and non-lactating animals. Lactating mares took more bites only in grassy and rough vegetation and they did this only in patches with a short sward height. In addition, lactating mares took more bites of grasses only and not of forbs or woody plants. We conclude that the extra grazing effort of the lactating animals was not distributed randomly. Lactating mares invested their extra grazing effort principally in those items that are the most grazed ones by the equids in general. We propose some hypotheses to explain why lactating mares increase their bite rate instead of augmenting the time spent grazing.

Introduction

The nutritional requirements of horses are influenced by a large number of factors such as body size, age, condition, health and reproductive state (Pilliner, 1999). The effect of reproduction on energy requirements varies with reproductive state. During the first 8 months of gestation, requirements for mares do not differ from those for maintenance. Energy requirements increase steadily during the last trimester of gestation, when they reach values that are 20% above maintenance levels. The protein requirements increase to 32% above maintenance levels, and there are high demands for calcium and phosphorus (data for 200-kilogram mares; NRC, 1989). Lactation is nutritionally far more demanding for the mare than is gestation. Although there is no agreement about the influence of the mare's intake on the foal's growth (Doreau and Boulot, 1989), it is generally accepted that the production of milk poses high nutritional demands on the lactating mares, especially during the first 3 months of the lactation period (NRC, 1989), when the amount of digestible energy and crude protein in the diet surpass with respectively 86% and 132% the demands for maintenance. As lactation progresses the demands decrease but remain higher than the maintenance requirements. In addition, the needs for calcium and phosphorus by lactating mares are more than double than those for non-lactating mares (NRC, 1989).

It is expected that free-ranging lactating horses modify their foraging behaviour to meet the increased nutritional requirements. Thus, lactating mares may graze for longer periods of time, graze faster, take bigger bites or may select a higher quality diet. Surprisingly, these issues have been considered only very rarely and often superficially in horses (Duncan, 1980; Duncan, 1985; Rittenhouse, 1986; Canacoo and Avornyo, 1998; Moehlman et al., 1998; Vulink, 2001; Ruckstuhl and Neuhaus, 2002; see Discussion), although more detailed studies were done with ruminants (e.g., Parsons et al., 1994; Penning et al., 1995; Gibb et al., 1999). We present results of a preliminary study that explored differences in grazing behaviour between lactating and non-lactating free-ranging equids. Our study subjects were two species of small equids, Shetland ponies (*Equus caballus*) and Donkeys (*Equus asinus*), which were grazing in dune habitats. We predicted that lactating animals would achieve a greater energy intake by grazing longer

and/or biting faster, and hence take more bites than non-lactating mares. Free-ranging animals have to make many foraging decisions at different levels (Senft et al., 1987). These are not only influenced by changes in the animal's needs, but also by factors such as forage availability and quality, which are in turn determined by environmental conditions. Previous studies reported the influence of seasonality and vegetation features on the grazing behaviour of free-ranging equids in temperate regions (Putman et al., 1981; Pratt et al., 1986; Gordon, 1989; Duncan, 1983; Duncan, 1992; Cosyns et al. 2001; Menard et al., 2002). In general, free-ranging equids show a decreased grazing activity in summer compared to winter. Although they forage preferably in grasslands year round, they increase foraging activity in scrub and woodland during autumn and winter. Therefore, putative differences in grazing behaviour between lactating and non-lactating mares might be affected by seasonality and vegetation characteristics.
Consequently we include in our analyses the possible effects of season and vegetation characteristics (composition and height) on grazing behaviour.

Materials and Methods

Study area and animals

We performed our study at two nature reserves ("Houtsaegerduinen" and "Westhoek") located in the coastal dune area of Belgium, Europe. In both areas domesticated grazers were introduced as a nature management tool. Both reserves are located in a coastal region with mild winters and mild summers. Mean annual temperature is 9.8°C. In summer, autumn, winter and spring mean temperature is 15.9°C, 10.8°C, 3.9°C and 8.7°C, respectively. Mean monthly precipitation is 60.7mm, 74.8mm, 56.5mm and 48.5mm, respectively (means over the period 1963-2002; Meteo WVL vzw).
In the "Houtsaegerduinen" a herd of donkeys (*Equus asinus*) graze throughout the entire area of the reserve (total area 80 ha). This site is mainly occupied by *Hippophae rhamnoides*/*Ligustrum vulgare* scrub, with relatively small and scattered patches of dune grassland and grey dune (*Cladonio-Koelerietalia*). Old, deteriorating *Hippophae* scrub is generally replaced by species-poor grassland dominated by *Calamagrostis epigejos*. Part of the area

has been planted with *Alnus glutinosa* and several non-native tree species (*Populus* div. spp.). For drinking the donkeys have access to two water pools, located more or less centrally in the reserve.
The "Westhoek" 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. A herd of Shetland ponies (*Equus caballus*) grazes in a fenced area (ca. 60 ha) encompassing a dune slack zone and an inner dune ridge. More or less closed vegetation covers two thirds of this area: main shrub species are *Hippophae rhamnoides*, *Ligustrum vulgare*, *Crataegus monogyna* and *Sambucus nigra*; tree species are *Populus x canadensis, Populus canescens, Ulmus minor* and *Alnus glutinosa*. The other third of the fenced area is occupied by grassland and herbaceous vegetation: species-rich dune grassland; tall herb vegetation with *Cirsium arvense*, *Eupatorium cannabinum*, *Lysimachia vulgaris, Lythrum salicaria* or *Iris pseudacorus*; patches of species-poor grassland enclosed by scrub, dominated by *Calamagrostis epigejos*; grey dune and some marram dune (*Ammophila arenaria)* vegetation. The ponies have access to several water pools to drink.

In both areas grazing started in April 1997. When field observations for the present study started during summer 2000, 15 donkeys (1 adult stallion, 1 stallion of two years, 1 male yearling, 5 adult mares, 2 mares of two years, 2 female yearlings and 3 male foals) were present in "Houtsaegerduinen" and 19 ponies (1 adult stallion, 3 stallions of 2 years, 1 male yearling, 8 adult mares, 2 mares of two years, 2 female yearlings and 2 male foals) and 4 Highland cattle were grazing in "Westhoek". In both study areas, the animals are free-ranging, graze year round and get no additional food.
In "Houtsaegerduinen" two donkey mares that foaled in June 2000 were chosen as the focal lactating animals. During the observation period these females were also pregnant, as they both foaled again in July 2001. Two adult mares that never foaled were chosen as the non-lactating, non-pregnant (further called "dry") mares. Body weight of the four donkey mares was measured in May 2000 and again in March 2001. The two lactating mares weighed 168.5 kg and 176.5 kg in 2000 and 143.5 kg and 162.5 kg in 2001; the non-lactating mares weighed 187.5 kg and 181.5 kg in 2000 and 178 kg and 180.5 kg in 2001.

In “Westhoek” there were only two lactating pony mares present in 2000; their foals were born in March and April 2000. Both were pregnant again and foaled in April 2001. Because all adult and two-year old females were pregnant, we choose the two yearling females as the non-lactating, non-pregnant mares. There are no data available of the body weights of the focal animals.

Weaning of all the donkey and pony foals occurred naturally, so the mares nursed their foals until a few months before the next foals were born.

Behavioural observations

Data were collected through continuous focal animal observation (Altmann, 1974). From August 2000 until July 2001 we conducted 39 and 35 sessions of 6 hours continuous observation at “Houtsaegerduinen” and “Westhoek”, respectively (3 or 4 sessions per month; two observers were involved in the data collection). For practical reasons all observations took place during daylight (between 6.00h and 19.00h). Before the start of each session we chose at random a lactating and a dry individual out of those selected for this study. We then continuously monitored the behaviour of one focal animal during a one-hour period and then switched to the other animal. This was repeated three times, such that each observation session covered 6 one-hour periods. If the two focal animals were not grazing in the neighbourhood of each other, we observed the same animal during three successive hours and subsequently located the other individual and observed it during the following three hours. Most of the animals in both study areas are habituated to the presence of humans and can be approached closely (1 m) without appreciably influencing their behaviour.

We recorded the start and end time (accuracy: 1 s) of the observed behaviours, as well as vegetation type and sward height, on a protocol form. Behavioural acts recorded are grazing, drinking, walking, standing alert, resting upright, laying down, rolling, grooming, mutual grooming, nursing, defecating, urinating, sniffing, scratching with hoof in soil, aggression, interactive behaviour, flehming, sexual activity. For the present study we only considered the grazing behaviour. Additionally, while a horse was grazing, we recorded plant species eaten and the number of bites taken (using a mechanical counter, 4 digits).

The different vegetation types distinguished in the field (n=18) were grouped into five vegetation units: ‘grassy vegetation’, ‘grass with shrub invasion’, ‘rough vegetation’, ‘scrub’ and ‘woodland’. For sward height we use a scale related to the animal’s physiognomy: ‘no height’ (in case of no vegetation), ‘shortly grazed’, ‘hoof’, ‘knee’, ‘belly’, ‘spine’ and ‘higher’.

All plant species eaten were grouped into four forage classes: ‘grasses’ (grasses in the strict sense, sedges and rushes), ‘forbs’, ‘woody plants’ and ‘other’ (e.g. mosses and ferns, unidentified plant species, soil).

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).

Data analysis

Grazing behaviour

We analysed data for donkeys and ponies separately. Interspecific differences could not be investigated at a quantitative level, since both equid species forage in different areas.

We quantified aspects of grazing behaviour of the equids with the variables ‘grazing time’, ‘number of bites’ and ‘bite rate’ (i.e., number of bites / minute grazing) and calculated their average value for combinations of lactation state and vegetation unit (or height category or forage class) per day (i.e., 3 hrs observation period). Because the animals were grazing mostly in patches where a mix of forage classes (e.g. grasses and forbs) were available, it was impossible to record the time that an animal was grazing a specific plant class. Therefore, we could not estimate grazing time and bite rate per forage class.

To calculate mean grazing time and number of bites, we included zero values. Thus, when on a given day an animal did not graze in a given vegetation unit (or height category or forage class), grazing time and number of bites were set to zero. This is appropriate because we can reasonably assume that an animal can potentially graze in all vegetation units (or height categories or forage classes) within a single observation period. Bite rate is dependent on the variables ‘number of bites’ and ‘grazing time’. However, we wanted to consider this third variable, and obtain additional information, by working with ‘effective’ bite rate in a vegetation unit or height category. Therefore, we did not include zero values for calculating mean bite rate, and so we considered this variable only when the horses were actually grazing in that vegetation unit or height category.

Statistics

We used mixed-models ANOVA to investigate the effects of the fixed factors ‘lactation state’, ‘vegetation unit’, ‘sward height’, ‘season’ and ‘forage class’ (only for number of bites) and their interactions, on the variation in grazing time, number of bites and bite rate. A repeated statement is used to take into account that the individual animals were sampled more than once. Because differences in grazing behaviour may exist between individual animals, we initially included a random factor with ’Individual’ as subject in our ANOVA model. 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.

Our data often do not meet the main assumptions of ANOVA (i.e., normality of distributions and homogeneity of variances), mainly because we include zero values and simultaneously consider various factors.

Unfortunately, there is no nonparametric alternative for ANOVA that satisfactorily deals with interactions between fixed factors on the one hand, and random factors on the other. Hence, we rely on the robustness of ANOVA when its assumptions are violated (Neter et al., 1996: p. 776-777), and are cautious in interpreting the results, especially when significance values approach $p = 0.05$.

Analyses are performed using SAS System V8. Number of degrees of freedom is estimated by the Satterthwaite-method.

Results

Grazing behaviour in all vegetation units

The time spent grazing by donkeys is significantly influenced by the factors vegetation unit and season, and by their interaction effect. Although lactation state does not significantly affect grazing time, the effect of the interaction between lactation state and vegetation unit is significant (Table 3.1). Figure 3.1 shows that lactating mares spend more time grazing in grassy vegetation than dry mares, but no differences are apparent in the other vegetation units.

The number of bites taken per three hours by grazing donkeys is significantly influenced by lactation state, vegetation unit, and by the interaction effects between lactation state and vegetation unit and between vegetation unit and season (Table 3.1). Overall, lactating donkeys take more bites than dry mares (Table 3.2). However, the significant effect of the interaction between lactation state and vegetation unit indicates that this difference varies among vegetation units, and is indeed only pronounced in grassy vegetation (Fig. 3.2).

The bite rate of grazing donkeys is significantly influenced by lactation state, vegetation unit and season, but not by the interaction effects between these factors (Table 3.1). Hence, lactating mares exhibit a higher bite rate than dry mares in all vegetation units, in all seasons (Table 3.2).

For the ponies, grazing time is significantly affected by vegetation unit, the interaction between vegetation unit and season and between lactation state and vegetation unit, although there is no significant effect of lactation state on grazing time (Table 3.1). Lactating pony mares spend more grazing time than dry mares in rough vegetation only (Figure 3.1).

Lactation state, vegetation unit, the interaction between lactation and season and between lactation and vegetation unit have significant effects on the number of bites taken by ponies (Table 3.1). Lactating ponies take more bites than dry mares (Table 3.2), but this difference is only apparent in rough vegetation (Figure 3.2).

Bite rate by the ponies is significantly affected by the interaction between lactation state and season, and by the factors lactation state, season and vegetation unit (Table 3.1). The number of bites taken per minute grazing is higher in lactating ponies than in dry pony mares (Table 3.2). There was also a significant effect of the random factor Individual, hence we did not eliminate this factor from the statistical model.

We separately considered the number of bites taken to different food classes. The analyses yield comparable results for the donkeys and ponies (Table 3.3). Variation in the number of bites is primarily induced by the factors lactation state and food class, and by the interaction between food class and lactation state (Table 3.3). In both donkeys and ponies, lactating mares take more bites than dry mares, but this difference is only apparent when they foraged on grasses (Figure 3.3). In the case of the ponies there is variation between individuals because we found a significant effect of the random factor Individual.

Grazing behaviour in grassy and rough vegetation

Both donkeys and ponies spend most time grazing in grassy and rough vegetation. These vegetation units also show the highest variability in sward height. Therefore, we examined whether lactation state has an effect on the sward height utilised by grazing animals in these two vegetation units only.

In donkeys, lactation state and its interactions with other factors has no significant effect on grazing time in grassy vegetation and rough vegetation (Table 3.4). The number of bites taken by donkeys is significantly influenced by the factors lactation state, sward height and season, and by the interaction between lactation state and sward height (Table 3.4). In grassy vegetation and rough vegetation donkeys take more bites at 'hoof height' and this is especially the case for the lactating mares (Figure 3.4). Bite rate of donkeys is affected by lactation state, sward height, but not by their interaction (Table 3.4). In grassy vegetation and rough vegetation lactating mares achieve a higher bite rate than dry mares.

In ponies, there is no significant effect of lactation state and of its interactions with other factors on grazing time in grassy vegetation and rough vegetation (Table 3.4). The number of bites that ponies take in grassy vegetation and rough vegetation is affected by lactation state, sward height and the interaction between lactation and sward height (Table 3.4). Lactating mares take more bites than dry mares in shortly grazed and hoof-height vegetation, but no differences are apparent in the higher height categories (Figure 3.4). Bite rate of ponies is affected by lactation state and sward height, but not by their interaction (Table 3.4). In grassy vegetation and rough vegetation lactating mares achieve a higher bite rate than dry mares.

Discussion

The main objective of the present study was to examine differences in grazing behaviour between lactating and dry free-ranging equids. We expected that the higher nutritional requirements of lactating animals (Pilliner, 1999) would induce modifications in their grazing behaviour. Assuming that lactating and non-lactating mares have the same digestive abilities (Rittenhouse, 1986), lactating animals should achieve a greater intake of organic matter and/or should select a diet with higher energy and protein content. A greater intake can be obtained by grazing longer, by biting faster and/or by taking bigger bites. A more nutritive diet can be achieved by selecting the most nutritive plants and plant parts; this selection can be made at the level of the vegetation as well as at the level of the individual plant.
The small sizes of the herds that we studied, forced us to observe a same small number of individual horses repeatedly, so the results are prone to pseudoreplication and may not be applicable to equids in general. The differences that we attribute to lactation state may reflect individual differences induced by some other factor, e.g. age in case of the ponies. However, our interpretation is strengthened by the highly similar results that we obtained for the two species studied, even though they foraged in different areas and differed in several components of their foraging behaviour. Nevertheless, our results should be considered as circumstantial and we encourage further studies based on a larger number of lactating and non-lactating animals.

Our results suggest that in both donkeys and ponies, lactating animals do not spend more time grazing than non-lactating mares. By contrast, lactating mares take ca. 50% more bites and increase their bite rate by 37% and 46% in donkeys and ponies respectively. Because we have no data on bite mass, we cannot examine the contribution of possible differences in bite

mass to the daily energy intake of lactating and non-lactating mares.
The observed differences between lactating and non-lactating animals in number of bites and bite rate are influenced by other factors. The observed differences between lactating and dry mares vary clearly among vegetation units. Lactating donkeys achieve a higher number of bites in grassy vegetation only, while lactating ponies do so in rough vegetation only. Moreover, the increase in number of bites taken by lactating mares in grassy vegetation and rough vegetation is especially pronounced in shortly grazed and hoof-high patches. It is known that forage in short patches has a higher digestibility (Van Soest, 1982; WallisDeVries and Daleboudt, 1994), and that grazing animals in general select for young growth and reject senescent plant material (McNaughton, 1984). Our observations indicate that lactating mares increase the number of bites taken particularly in shortly grazed patches. We hypothesize that this behaviour will not allow the lactating mares to obtain a much increased intake of biomass, but rather that they achieve a higher proportion of high quality forage, which is rich in proteins. This would contribute to meet the much increased protein requirements for lactating mares (NRC, 1989).
Horses are considered as grazers that feed predominantly on grasses (Van Dyne et al., 1980; Putman et al., 1987; Duncan, 1992; Hoffmann et al., 2001; Cosyns et al., 2001; Vulink, 2001). Our results indicate that lactating mares select even more strongly for grasses: they increase their number of bites by taking more bites of grasses only, and not of forbs or woody plants (proportion of grasses in the diet, for donkeys: Lactating: 81.4% versus Dry: 75.0%, for ponies: Lactating: 95.1% versus Dry: 90.7%).

Results of the scarce studies that investigated the differences in grazing behaviour between lactating and non-lactating mares showed that lactating mares do not significantly increase the time spent grazing (Duncan, 1980 [2]; Canacoo and Avornyo, 1998; Moehlman et al., 1998; Ruckstuhl and Neuhaus, 2002). These findings coincide with our results. Only Ruckstuhl and Neuhaus (2002) investigated bite rate besides foraging time and concluded that lactating zebra mares have higher bite rate than non-lactating mares, which is in line with our findings for donkeys and Shetland ponies. Nevertheless, Vulink (2001) who studied two reproductive and one non-reproductive Konik horses which were free-ranging in a highly productive area, reported contrasting results. He concluded that the lactating mares foraged significantly longer than the dry mares. Moreover, the number of bites taken of various forage classes was similar between reproductive and non-reproductive horses, indicating an almost identical diet composition and hence a highly similar content of digestible organic matter in their diets. Hence, the higher demands of the lactating Konik mares were met through a higher estimated daily digestible energy intake, achieved by feeding longer (Vulink, 2001).

Why do the lactating mares in the present study not increase their grazing time rather than augmenting their bite rate? Free-ranging horses and ponies graze in bouts, separated by periods of non-grazing activity (Tyler, 1972; Francis-Smith, 1977). When a horse is grazing, oropharyngeal stimuli are enough to induce satiety and to end a meal. However, gastrointestinal stimuli control the duration of satiety (Ralston, 1984) and a horse will not start a new feeding bout as long as these stimuli are not given. This physiological constraint, and the necessity to perform other behaviours (resting, travelling, reproductive behaviour, etc.), will result in an upper limit for grazing time. In areas with low forage quantity or quality horses can graze up to 75% of their total activity time (Putman et al., 1981). Our study was conducted in dune areas with low plant productivity. The dry ponies grazed for 69% of the time, such that lactating mares can augment their grazing time by only limited amounts. We, therefore, hypothesize that lactating ponies must increase their bite rate to meet their higher energy demands. This grazing time constraint hypothesis does however not apply to the donkeys in our study. In a study in Ghana, donkeys spent 80% of their time grazing during the day (Canacoo and Avornyo, 1998). In our study, lactating donkeys graze up to 58% of their activity time, which seems to be well below the upper threshold value for grazing time. Why then do the lactating donkeys not further increase their grazing time? We hypothesize that the highly synchronous foraging behaviour that is manifest in herds of equids (Boyd and Bandi, 2002) acts as a behavioural limit to a further increase in grazing time by the lactating mares.
An additional consideration derives from the optimal foraging theory which

assumes that an animal should maximize its long-term intake rate of energy and other essential nutrients by making a trade-off between gains from energy intake in different patches and costs in time and energy for travel, searching and food handling (Stephens and Krebs, 1986). Assuming that our study animals obtain an optimal balance between costs and gains, we propose that the net proceeds of biting faster are higher than the net gains of an increased grazing time in the lactating animals. Further studies are however needed to test these hypotheses.

Acknowledgements

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Table 3.1

Results of the ANOVA-model examining the effects of the factors 'lactation state', 'vegetation unit' and 'season' on the variables 'grazing time', 'number of bites' and 'bite rate' for donkeys and ponies. Shown are the final models after elimination of non-significant 3-way and 2-way interactions.

			Grazing Time			**Number of Bites**			**Bite Rate**		
		df1	**df2**	**F**	**P**	**df2**	**F**	**P**	**df2**	**F**	**P**
Donkeys	Lactation	1	155	1.44	0.232	139	11.05	**0.001**	228	11.79	**<0.001**
	Vegetation	4	245	13.52	**<0.001**	235	19.50	**<0.001**	228	10.04	**<0.001**
	Season	3	167	3.79	**0.012**	152	1.62	0.187	228	6.52	**<0.001**
	Vegetation *Season	12	257	3.32	**<0.001**	240	2.93	**<0.001**			n.s.
	Lactation *Vegetation	4	245	2.51	**0.042**	233	6.17	**<0.001**			n.s.
	Lactation *Season	3			n.s.			n.s.			n.s.
	Lactation *Vegetation *Season	12			n.s.			n.s.			n.s.
Ponies	Lactation	1	121	0.27	0.607	305	10.89	**0.001**	10.7	25.07	**<0.001**
	Vegetation	4	223	68.62	**<0.001**	305	72.70	**<0.001**	162	16.41	**<0.001**
	Season	3	132	1.49	0.221	305	0.27	0.844	10.6	3.97	0.039
	Vegetation *Season	12	226	7.19	<0.001	305	5.39	**<0.001**			n.s.
	Lactation *Vegetation	4	222	2.77	**0.028**	305	7.93	**<0.001**			n.s.
	Lactation *Season	3			n.s.			n.s.			n.s.
	Lactation *Vegetation *Season	12			n.s.			n.s.			n.s.

Table 3.2

Grazing behaviour of dry and lactating donkeys and ponies. Null values are included for the calculation of mean grazing time and mean number of bites (per 3 hours).

		GrazingTime (min.)			Number of bites			Bite Rate (bites/min.grazing)		
		Mean	SE	N	Mean	SE	N	Mean	SE	N
Donkeys	dry	90,87	5,54	39	797	70	37	8,68	0,44	37
	lactating	102,95	5,78	39	1250	100	37	12,22	0,86	37
Ponies	dry	123,85	4,74	35	2340	151	33	18,88	1,06	33
	lactating	130,19	4,07	35	3559	184	33	27,66	1,27	33

Table 3.3

Results of ANOVA-model examining the effects of the factors 'lactation state', 'food class' and 'season' on the variable 'number of bites' taken by donkeys and ponies. Shown are the final models after elimination of non-significant 3-way and 2-way interactions.

			Number of Bites		
		df1	df2	F	P
Donkeys	Lactation	1	213	11.05	**0.001**
	Class	2	213	119.65	**<0.001**
	Season	3	213	2.08	0.104
	Class*Season	6			n.s.
	Lactation*Class	2	213	9.02	**<0.001**
	Lactation*Season	3			n.s.
	Lactation*Class*Season	6			n.s.
Ponies	Lactation	1	4.17	10.14	**0.031**
	Class	2	5.62	157.18	**<0.001**
	Season	3	6.98	0.58	0.648
	Class*Season	6			n.s.
	Lactation*Class	2	5.62	9.54	**0.016**
	Lactation*Season	3			n.s.
	Lactation*Class*Season	6			n.s.

Table 3.4

Results of the ANOVA-model examining the effects of the factors 'lactation state', 'sward height' and 'season' on the variables 'grazing time', 'number of bites' and 'bite rate' for donkeys and ponies, grazing in grassy vegetation and rough vegetation. Shown are the final models after elimination of non-significant 3-way and 2-way interactions.

			Grazing Time			Number of Bites			Bite Rate		
		df1	**df2**	**F**	**P**	**df2**	**F**	**P**	**df2**	**F**	**P**
Donkeys	Lactation	1	369	0.85	0.356	114	5.83	**0.017**	46.8	7.66	**0.008**
	Height	4	369	16.05	**<0.001**	245	12.52	**<0.001**	152	3.23	**0.014**
	Season	3	369	1.30	0.274	122	3.12	**0.028**	62.8	3.32	**0.025**
	Height*Season	12	369	2.83	**0.001**			n.s.			n.s.
	Lactation*Height	4			n.s.	254	2.70	**0.031**			n.s.
	Lactation*Season	3			n.s.			n.s.			n.s.
	Lactation*Height *Season	12			n.s.			n.s.			n.s.
Ponies	Lactation	1	134	3.76	0.054	124	17.55	**<0.001**	9.35	10.07	**0.011**
	Height	4	213	91.63	**<0.001**	203	85.92	**<0.001**	136	22.96	**<0.001**
	Season	3	140	2.52	0.061	129	0.74	0.526	11.9	1.68	0.224
	Height*Season	12	219	2.17	**0.014**			n.s.			n.s.
	Lactation*Height	4			n.s.	203	6.75	**<0.001**			n.s.
	Lactation*Season	3			n.s.			n.s.			n.s.
	Lactation*Height *Season	12			n.s.			n.s.			n.s.

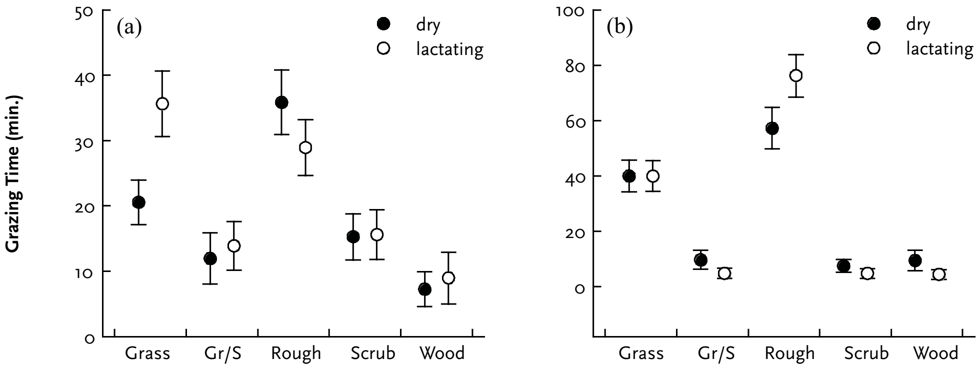

Figure 3.1

Mean (± 1 SE) grazing time by lactating (open symbols) and dry animals (solid symbols) in distinct vegetation units for donkeys (a) and ponies (b). Vegetation units: Grassy vegetation (Grass), Grass/Shrub (Gr/S), Rough vegetation (Rough), Scrub, Woodland (Wood). Note that the Y-axes of the two panels have different scales.

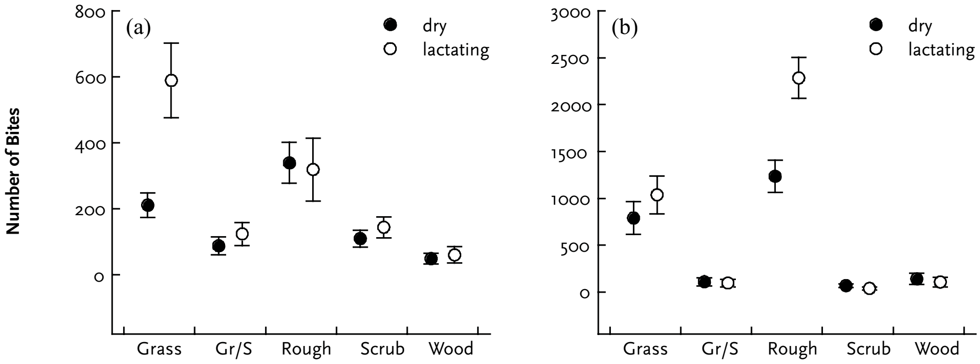

Figure 3.2

Mean (± 1 SE) number of bites (per 3 hrs) taken by lactating (open symbols) and dry animals (solid symbols) in distinct vegetation units for donkeys (a) and ponies (b). Vegetation units: Grassy (Grass), Grass/Shrub (Gr/S), Rough vegetation (Rough), Scrub, Woodland (Wood). Note that the Y-axes of the two panels have different scales.

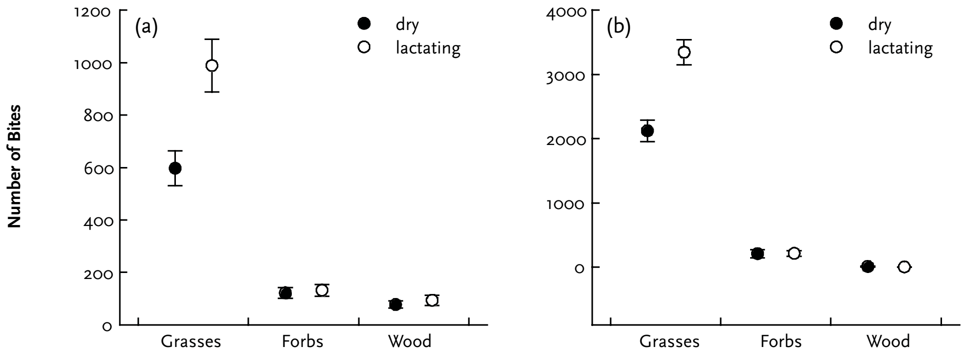

Figure 3.3
Mean (± 1 SE) number of bites (per 3 hrs) taken by lactating (open symbols) and dry animals (solid symbols) of distinct forage classes for donkeys (a) and ponies (b). Note that the Y-axes of the two panels have different scales.

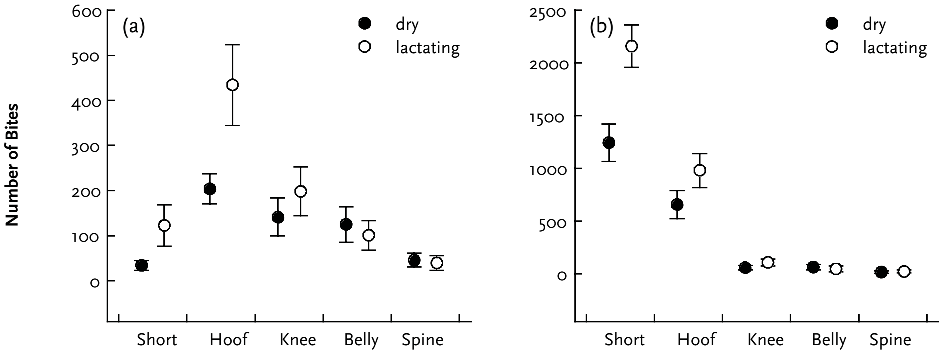

Figure 3.4
Mean (± 1 SE) number of bites (per 3 hrs) taken by lactating (open symbols) and dry animals (solid symbols) of vegetation of distinct height categories in donkeys (a) and ponies (b). Height categories: Shortly grazed (Short), Hoof, Knee, Belly, Spine. Note that the Y-axes of the two panels have different scales.

4

Eliminative behaviour of free-ranging horses: do they show latrine behaviour or do they defecate where they graze?

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The fungus *Poronia erici* on horse dung, Ghyvelde (foto: Ruben Walleyn)

Abstract

In contrast to horses in pastures, it is thought that free-ranging horses do not perform latrine behaviour, i.e. a behavioural pattern whereby the animals graze and defecate in separate areas. However, few studies deal with this particular subject, reporting contrasting conclusions. We hypothesize that horses free-ranging in large heterogeneous areas do not perform latrine behaviour. Thus, we believe that grazing and elimination behaviour are spatially related: where horses graze, they will also defecate. Behavioural data were collected from Konik horses, Haflinger horses, Shetland ponies and donkeys, grazing in different nature reserves (54-80 ha). Data for the different equids were analysed separately, as well as data for mares and stallions (Konik and donkey stallions only). We investigated the proportion of the number of defecations/urinations while grazing on the total number of defecations/urinations. Furthermore, we searched for the sequence of behaviours representing latrine behaviour in the strict sense. Additionally, we analysed the correlation between grazing behaviour and eliminative behaviour on both vegetation type level and patch level. All the female equids often continued grazing while defecating. During urination, grazing ceases in the majority of instances. Cases where a mare terminated grazing in a certain vegetation type and sward height, to eliminate in another vegetation type or in another sward height within the same vegetation type were rarely observed. On the vegetation type level as well as on the patch level, there was a highly significant ($p < 0.001$) positive correlation between grazing time and number of eliminations (or eliminating time). The high values of the correlation coefficients (in case of the defecation variables r ranges between 0.553 and 0.955; in case of the urination variables r ranges between 0.370 and 0.839) illustrate that the spatial distribution of eliminative behaviour can be explained to a high degree by the spatial distribution of grazing behaviour. Results in the case of the stallions are preliminary, but indicate the same pattern. Hence, horses, free-ranging in large heterogeneous areas, do not perform latrine behaviour, but defecate where they graze. Possibly, animal density is of major importance to explain this behavioural difference with horses in pastures. We suggest that also spatial vegetation heterogeneity and plant productivity of the grazed area, as well as parasite status of the grazing animals could play a role to explain the non-appearance of latrine behaviour.

Keywords: Equids, faeces avoidance, grazing behaviour, spatial differentiation, urine, horse marking

Introduction

Free-ranging herbivores have 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. These decisions are primarily made in relation to forage availability and quality, which are in turn determined by environmental conditions. On the other hand large herbivores themselves have an impact on their environment as well. Grazing animals affect the plants they utilize for forage in an enhancing or a degrading way (Vallentine, 1990; Briske, 1991). Furthermore, large herbivores have an impact on a higher level of ecological resolution. Herbivores can influence diversity, density and productivity of a plant community (Vallentine, 1990; Archer & Smeins, 1991; Duncan, 1992; Bakker, 1998), mainly through their selective grazing, but also through other behaviour like trampling and rolling. Also the eliminative behaviour of large herbivores is brought up as a potential factor playing a role in both vegetation development (Archer, 1973; Steinauer & Collins, 1995; Bokdam et al., 2001) and foraging strategy (Marten & Donker, 1964; Ödberg & Francis-Smidt, 1976; Archer, 1978; Hutchings et al., 1998). Captive horses in pastures are known to establish a pattern of shortly grazed patches, relatively free of faecal droppings, and ungrazed taller patches, where horses preferably defecate and urinate (Archer, 1972; Archer, 1973; Ödberg & Francis-Smith, 1976). This pattern is caused by the avoidance of grazing near faecal droppings (Ödberg & Francis-Smith, 1977; Archer, 1978), and not through an initial difference in palatability of the vegetation of the grazed and ungrazed patches (Ödberg & Francis-Smith, 1977). It is suggested that this behaviour is a result of diminishing the chances of helminthic reinfestation (Taylor, 1954; Arnold & Dudzinski, 1978). Recently, this hypothesis is experimentally tested and confirmed in the case of sheep (Hutchings et al., 1998; Hutchings et al., 2002). Studies on the behaviour and/or habitat use of free-ranging or feral horses rarely discuss the horses' eliminative behaviour. Tyler (1972) reported some aspects of the eliminative behaviour of ponies in the New Forest. One conclusion was that there was no evidence that the ponies grazed and defecated in separate areas. Several authors (Tyler, 1972; Boyd, 1998; Klingel, 1998; Moehlman, 1998) mentioned specific eliminative behaviour of stallions as part of scent marking behaviour. Moehlman (1998) stated that, in contrast with donkey stallions, female donkeys of all ages showed little interest in dung and simply defecated where they stood. Only Edwards & Hollis (1982) dealt with the subject of the eliminative behaviour of free-ranging horses in particular. They concluded that the establishment of distinct latrine areas by horses is not merely a result of captivity, but does occur in free-ranging animals.

In several coastal nature reserves, close to the French-Belgian border, several different equids are free-ranging for nature management reasons. An initial investigation of the areas did not provide any visual cue to suppose that the above-mentioned latrine behaviour induced patterns were created. There were some faecal concentrations on paths and on frequently used resting places or grazing spots. We supposed that the faecal piles on paths were the result of the marking behaviour of the stallions. Other concentrations of defecations were believed to be the result of a concentration of animals in space and time. Between 1998 and 2001 we made numerous behavioural observations on the different free-ranging equids in these nature reserves. Based on these observations we hypothesized that horses grazing in large heterogeneous areas, do not perform ”latrine behaviour”. We defined “latrine behaviour” as follows: a horse stops grazing and walks to an “eliminative” or “latrine” area to defecate or urinate, afterwards the horse walks back to a “nutritive” area (as described by Ödberg & Francis-Smith, 1976), or sometimes grazes in the “latrine” area for a while, and then gradually moves back to the “non-latrine” area (as described by Edward & Hollis, 1982). A more indirect way to examine the occurrence of latrine behaviour was to investigate the spatial relation between grazing and defecating/urinating. A strong positive relationship between grazing and eliminative behaviour would indicate that latrine areas are not formed.

Materials and Methods

Study sites

We performed our study at three nature reserves ("Westhoek", "Houtsaegerduinen" and "Ghyvelde"). The first two are located in the coastal dunes of Belgium, near the French border. The latter is an old dune area in France close to the northern French coastline and bordering an equally old dune ridge in Belgium. All these reserves are relatively nutrient poor systems with a spatially heterogeneous vegetation pattern. Domesticated grazers were released as a nature management tool, in the entire reserve or in parts of it.

The "Westhoek" 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. A fenced area in the north of the reserve ("Westhoek-North", 54 ha) is grazed by a herd of Konik horses and a small group of Highland cattle. Scrubs of *Hippophae rhamnoides* L. (Sea Buckthorn), *Ligustrum vulgare* L. (Wild Privet) and to some lesser extent *Salix repens* L. (Creeping Willow) occupy the largest part of the area. Before the start of the grazing project 12% of the original 79% scrub layer was cut down and removed, resulting in an area of ruderal vegetation composed of a low, grass-dominated layer (main species are *Holcus lanatus* L. (Yorkshire-fog) and *Calamagrostis epigejos* Roth (Wood Small-reed)) and patches of tall herbs *Eupatorium cannabinum* L. (Hemp-agrimony), *Lythrum salicaria* L. (Purple Loosestrife) and *Cirsium arvense* Scop. (Creeping Thistle). The remaining area is covered by species-poor grassland, dominated by *Calamagrostis epigejos* or *C. canescens* Roth (Purple Small-reed); species-rich dune grassland with *Poa pratensis* L. (Smooth Meadow-grass), *Avenula pubescens* (Huds.) Dum. (Downy Oat-grass), *Veronica chamaedrys* L. (Germander Speedwell), *Galium verum* L. (Lady's Bedstraw); young dune slack and moss dune.

"Westhoek-South" (ca. 60 ha), a fenced area in the south of the "Westhoek" is grazed by a herd of Shetland ponies and a group of Highland cattle. The area encompasses a dune slack zone and an inner dune ridge. Two thirds of this area is covered by more or less closed scrub vegetation: main shrub species are *Hippophae rhamnoides, Ligustrum vulgare, Crataegus monogyna* Jacq. (Hawthorn) and *Prunus spinosa* L. (Blackthorn); tree species are several Poplar species (*Populus x canadensis* Moench, *Populus tremula* L., *Populus canescens* Smith), *Ulmus minor* Mill. (Small-leaved Elm) and *Alnus glutinosa* Gaertn (Alder). The other third of the fenced area is occupied by grasslands and herbaceous vegetations: species-rich dune grasslands with *Poa pratensis*, *Avenula pubescens*., *Veronica chamaedrys* and *Galium verum*; tall herb vegetation with *Cirsium arvense, Eupatorium cannabinum, Lysimachia vulgaris* L. (Yellow Loosestrife), *Lythrum salicaria* or *Iris pseudacorus* L. (Yellow Iris); patches of species-poor grassland enclosed by scrub, dominated by *Calamagrostis epigejos*; moss dune and some marram dune (*Ammophila arenaria* Link) vegetation.

In the "Houtsaegerduinen" a herd of donkeys graze all over the reserve (ca 80 ha). The site is mainly occupied by *Hippophae rhamnoides/Ligustrum vulgare* scrub, with relatively small and scattered patches of dune grassland and moss dune (*Cladonio-Koelerietalia*). Old, deteriorating *Hippophae* scrub is generally replaced by species-poor grassland dominated by *Calamagrostis epigejos*. Part of the area has been planted with *Alnus glutinosa* and several non-native tree species (*Populus* div. spp.).

In "Ghyvelde" (ca. 75 ha) a herd of Haflinger horses is grazing the entire area. Two thirds of this area is open habitat formed by *Carex arenaria* L.-dominated grassland (Sand sedge), alternated with moss dunes. One central forest and several dispersed, small congregations of trees shape the woodland at the site, which is mostly afforested. Additionally, the closed vegetation is also formed by natural scrub of *Hippophae rhamnoides, Ligustrum vulgare, Salix repens* and *Sambucus nigra* (Elder).

Animals

In all study areas, the animals are free-ranging and remain in the area year round. They receive no additional food. Nonetheless the herds are managed to avoid inbreeding and overgrazing. Each year all equids in the Belgian nature reserves were treated with 'Horseminth' (Pfizer), an anthelminthic active against a broad spectrum of gastro-intestinal parasites. Within the observation periods Konik horses were treated once and Shetland ponies and donkeys three times.

Grazing by Konik horses in “Westhoek-North” started in 1998 with two mares and two stallions. During the study period the herd was enlarged with one foal.

In “Westhoek-South” grazing started in April 1997, with seven Shetland pony mares and one stallion. The herd enlarged mainly naturally and at the end of the study period, in spring 2001, there were 17 adult ponies, two colt yearlings and 10 foals. The adult group was formed by one dominant stallion, 12 mares and four bachelor stallions (three geldings).

In “Houtsaegerduinen” a stallion and five donkey mares were introduced in 1997. Two more stallions and a mare were introduced later and 15 foals were born so that in spring 2001 there were nine mares, five stallions, three colt yearlings and seven foals.

At the initiation of the observations in “Ghyvelde” (May 2000) the herd of Haflinger horses was composed by four stallions, 11 mares and three foals. Composition of the herd changed twice, but during most of the observations 12 adult horses (three stallions, nine mares) and two foals were grazing the area. An overview of the animal density during the observation periods in the different areas is given in Table 4.1.

Behavioural observations

All observations took place between August 1998 and August 200l. Different periods of observations should be distinguished. Six observers (the six first authors of the paper) were involved in the data collection. Donkeys were observed: August 1998-March 1999 (0.00h-24.00h), August 1999-March 2000 (6.00h-24.00h), May 2000-July 2001 (daylight hours) (in total 1061 observation hours; mean observation frequency was 6, 5 and 6 sessions/month, respectively). Shetland ponies were observed during August 1998-March 1999 (0.00h-24.00h) and May 2000-July 2001 (daylight hours) (in total 706 observation hours; mean observation frequency was 6 and 5 session/month, respectively). Observations of Konik horses were carried out from August 1999 to March 2000 (6.00h-24.00h) (in total 297 observation hours; mean observation frequency was 7 sessions/month). Observations of Haflinger horses were performed from May 2000 to April

2001 (daylight hours) (in total 185 observation hours; mean observation frequency was 3 sessions/month).
Data were collected through continuous focal animal observation (Altmann, 1974). During a six-hour period we continuously monitored the behaviour of one focal animal, chosen at random from a pool of possible study animals. Observational data are from six donkey mares and one donkey stallion (born in the reserve April 1998; subordinate, but competing with his father for the dominant position), ten Shetland pony mares, two Konik mares and two Konik stallions (one dominant and one subordinate), and three Haflinger mares. The same individuals were repeatedly observed (for donkeys, Shetland ponies, Konik horses and Haflinger horses the mean number of observation periods per individual is 25, 12, 12 and 10 respectively). The observed individuals were habituated to the presence of humans and could be approached closely (1 m) without visible influence on their behaviour. The duration (accuracy: 1 s) of the observed behaviours and the vegetation type in which the behaviours were performed were recorded on a protocol form. From May 2000 onwards, we noted also height of the vegetation in which the behaviour was performed. 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'. We considered the behaviours grazing, resting up, laying down, walking, standing alert, grooming, mutual grooming, drinking, defecating, urinating, defecating while grazing, urinating while grazing, nursing, nursing while grazing, rolling, sniffling, pawing, flehming, aggressive behaviour, sexual activity and other interactions. When a grazing animal put its head upwards and it was not chewing, this moment was considered as the end of its grazing activity and the start of a subsequent behaviour.

Data analysis

Data from the different equid groups (in the different areas) were analysed separately. The different observation periods were analysed together. Data from mares and data from stallions were handled separately, as the eliminative behaviour of stallions could be expected to be influenced by marking behaviour. As we only had data from two Konik stallions and one donkey stallions, the results concerning stallions are only indicative.

Eliminative behaviour

First potential evidence for our hypothesis came from the observation that the horses often did not stop grazing to defecate and to a lesser degree even to urinate. To analyse this we retained the behaviours defecating, urinating, defecating while grazing and urinating while grazing. We calculated the proportion of the number of defecations while grazing over the total number of defecations (sum of the number of defecations and the number of defecations while grazing). The same procedure is followed for the number of urinations.

Furthermore we investigated whether the event of "latrine behaviour" did occur, by looking for the following sequence of behaviours: animal is grazing in a certain vegetation type with a certain height - animal stops grazing, doing other behaviours while moving to another vegetation type or to another sward height within the same vegetation type - animal defecates or urinates in that other vegetation type or sward height - animal performs another activity. We considered a maximum time of 60 seconds between the grazing stop and the start of the elimination, because we assumed that a horse would not walk for more than 60 seconds to a particular place to eliminate there. We retained also the two successive behaviours, occurring after the eliminative behaviour, to see whether the horse started grazing in the patch (with a certain vegetation type and sward height) where it was eliminating.

Spatial relation between grazing and eliminative behaviour

It could very well be that the mares did not perform latrine behaviour as described above, but that they concentrated their faecal droppings anyway in places where they grazed less, with the consequence that their favourite grazing places were less contaminated with faeces than the places where they spent less time grazing. Therefore, we investigated the spatial relation between grazing behaviour and eliminative behaviour. We supposed that the number of defecations (urinations) in a given vegetation type is a good measure for the quantity of faeces (urine) that this vegetation type receives. It is also possible that defecation time (urination time) is a better measure for the quantity of faeces (urine), therefore we analysed the questions below by two alternative approaches using either number of defecations (number of urinations) or defecation time (urination time) as dependent variables.

At the vegetation type level:

Per vegetation type we calculated the total time spent grazing and the total number of defecations (or urinations), and analysed correlations between these variables. Sample size (n) is the number of vegetation types. We did the same with total time spent defecating or urinating in a vegetation type.

At the patch level in the most grazed vegetation types:

Possibly, the pattern of latrine areas and non-latrine areas did not occur at the scale of the vegetation types, but rather at the scale of patches (combinations of vegetation types and sward heights). Therefore, we "zoomed in" to this more detailed scale. Avoidance of grazing near faeces would form the basis for the formation of latrine areas (Ödberg & Francis-Smith, 1977; Archer, 1978). We assumed that if the animals avoided places where faeces occurred, this would be most detectable in the vegetation types with highest grazing times, which we analysed consequently. We calculated total time spent grazing and total number of defecations (or urinations) per height class per vegetation type, and we again analysed the correlations. We did the same with total time spent defecating or urinating per height class per vegetation type. Since data on sward height were collected from May 2000 onwards, these analyses could only be done for donkeys, Shetland ponies and Haflinger horses.

At the patch level in a grassland entity:

In "Westhoek- South" a pasture-like area of 6.6 ha is intensively used by the ponies. We assume this situation comparable to the one studied by Edwards & Hollis (1982) in the New Forest. Within this grassland-entity several vegetation types and several sward heights within these vegetation types could be distinguished. We calculated the total time spent grazing and the total number of defecations (or urinations) per height class per vegetation type, and we analysed again the correlations between these variables. The same is done with total time spent defecating or urinating per height class per vegetation type.

Square root transformations were performed on all variables to achieve normal distributions. When transformed data had a truly normal distribution, Pearsons correlations were calculated, if not so, we used Spearman correlations. All analyses were performed using SPSS 11.0 for Windows.

Results

Eliminative behaviour

Defecating occurred more frequently than urinating in all equids (Table 4.2). All the female equids defecated often while grazing, i.e. 46-60% of all performed defecations (Table 4.2). In the other cases they were standing or walking while defecating. The two Konik stallions and the one donkey stallion mostly ceased grazing to defecate. We also found that in most cases grazing was stopped during urinating. Donkeys urinated very rarely while grazing, but Haflinger and Konik mares did so more frequently (Table 4.2). Shetland pony mares terminated grazing in a certain vegetation type and moved within 60 seconds towards another vegetation type and defecated there in only six of the 419 defecations. If they behaved this way, in two out of six times the pony mares subsequently started grazing in the vegetation type in which they defecated. Only one out of 299 times a pony mare changed vegetation type before urinating, though subsequently started grazing there afterwards. Donkey mares changed vegetation type four out of 609 times to defecate and six out of 259 times to urinate. In one of the four defecations and in three of the six urinations they started grazing in the vegetation type where they had eliminated. The donkey stallion changed six out of 68 times of vegetation type to defecate. In one of these six events the donkey stallion started grazing within the fouled vegetation type. In the case of the Haflinger horses a mare changed the vegetation type to urinate only once. In the case of the Konik horses we found none. One pony mare moved to another sward height, within the same vegetation type, to eliminate there. This was the only case of movement to another sward height

within the same vegetation type for all the equids studied this way (Shetland ponies, donkeys and Haflinger horses).
This minimal amount of movements to another vegetation type or to another sward height within the same vegetation type to defecate or urinate is considered rather to be coincidental than as evidence of latrine behaviour.

Spatial relation between grazing and eliminative behaviour

At the vegetation type level

For donkeys and the three other equid breeds we analysed the correlation between total grazing time in a vegetation type on the one hand and total number of defecations (urinations) and total defecation (urination) time in that vegetation type on the other hand. For the mares, we found a highly significant ($p < 0.001$) positive correlation for both defecating and urinating behaviour (Table 4.3; Figures 4.1 and 4.2). This means that vegetation types with a low grazing time encounter a low elimination activity, while vegetation types with a higher grazing time receive a higher number of defecations and urinations (and show a higher defecation time and urination time). Results of the Konik stallions were very similar compared to the results of the Konik mares (Table 4.3). In the case of the donkey stallion we also found highly significant positive correlations, though smaller values for the correlation coefficients (Table 4.3). In most cases, for both mares and stallions, the correlation coefficients were higher for the defecations than for the urinations. We conclude that the equids eliminated most in the vegetation types where they grazed most, and eliminated less in less grazed vegetation types.

At the patch level in the most grazed vegetation types

When considering different patches within the most frequently grazed and hence most frequently fouled vegetation types, the highly significant positive correlations remained (Table 4.4a). Patches with a small grazing time showed a small number of eliminations and patches with higher grazing times received a higher number of eliminations. Again, we found for the donkey stallion lower values for the correlation coefficients in comparison with the donkey mares.

At the patch level in a grassland entity

In “Westhoek-South” we analysed how the Shetland ponies used “The Pasture”, an intensively grazed part of the terrain. In this area different grass-dominated vegetation types could be distinguished. Within these vegetation types, different sward heights could be discriminated. Again we found highly significant positive correlations. Total grazing time in a vegetation type-sward height combination was positively correlated to total number of defecations/urinations and to total defecation/urination time in this vegetation type-sward height combination (Table 4.4b).

Discussion

In the present study we hypothesized that free-ranging horses do not perform latrine behaviour. Thus, these horses do not concentrate their eliminations in certain areas, where they avoid grazing. Our results confirm this hypothesis.

The mares often defecated while grazing, i.e. 46-60% of all performed defecations. This proportion was smaller for the observed stallions (7-20%). On the other hand mares and stallions mostly stopped grazing to urinate. Stalled ponies moved to another place before they defecated or urinated in 50% of the occasions (Sweeting et al., 1985). The differences in both eliminative behaviours can be due to the processes of the two eliminative behaviours themselves. Waring (2003) describes that a horse about to urinate adapt a basic posture, where the neck is slightly lowered, the tail is raised, and the hind legs are spread apart and stretched posteriorly. He reports also that during urination, grazing ceases in the majority of instances and no particular site is sought. Our findings are in line with Waring’s report. The process of defecation occurs without any specific posture except that the tail is raised and often held to one side (Waring, 2003). If the horse does not have to take up a specific posture it can proceed to graze without interruption.

We rarely observed an animal terminated grazing and started a subsequent behaviour while moving to another vegetation type or to another sward height within the same vegetation type, where it subsequently defecated or urinated. Therefore and because the horses, in particular the mares, often defecated while grazing, we conclude that the horses in the field situation of the present study did not perform latrine behaviour.

The only donkey stallion that was observed changed vegetation type to defecate in 8.8% of the cases. We believe this was not the result of latrine behaviour, but was merely a result of marking behaviour. Several authors reported specific eliminative behaviour of stallions, in pastures as well as in more natural surroundings (Tyler, 1972; Ödberg & Francis- Smith, 1976; Boyd, 1998; Klingel, 1998; Moehlman, 1998). Marking behaviour is the behavioural pattern to deposit chemical signals on environmental objects or other animals of the same species (Ralls, 1971). Marking behaviour in stallions occurs mainly with faeces and urine and occurs as well on established faecal piles as on the fresh excrements of mares (Kimura, 2001, Waring, 2003). Different functions have been attributed to it (Klingel, 1998; Kimura, 2001). Although we did not perform research on the marking behaviour of the stallions in particular, at this point we think it is worth mentioning some field observations. On several occasions we observed donkey stallions visiting established faecal piles. Both dominant and subdominant stallions inspected such piles. Olfactory inspection occurred by smelling and sniffing, sometimes followed by flehming. Often the stallions then deposited fresh faecal material to the existing pile, and a second bout of olfactory investigation completed this process. Stallions also urinated on top of a faecal pile. On some occasions we observed that several donkey stallions investigated faecal piles all together, and consecutively defecated on top of it. The sequence of stallions defecating on the faecal pile could be related to the dominance order of the males, although literature does not provide an unambiguous view on this (Waring, 2003). Also the two Konik stallions in “Westhoek-North” eliminated on established piles or fresh excrements of mares. In the case of the Shetland ponies and the Haflinger horses this behaviour was only rarely seen, probably due to the composition of the herds.

On the vegetation type level as well as on the patch level there was a highly significant positive correlation between the time spent grazing and the number of defecations and urinations. This means that there was no spatial differentiation between grazing behaviour and eliminative behaviour. The high values of the correlation coefficients in the cases of the four mare groups and the Konik stallions illustrate that the spatial variation in the number of defecations can be explained to a high degree by the spatial variation in grazing time. For the donkey stallion we found smaller values for the correlation coefficients. However, the range of the values on both the x- and the y-axes is considerably larger in mares than in stallions. It is known that the values of correlation coefficients are influenced by the range of the x- and y- axes (Smith, 1984). The values of the correlation coefficients for the urination variables were in most cases smaller than for the defecation variables. This may be due to the smaller range of the y-axes and/or to the presence of more null values (since the horses urinated less frequently than that they defecated).
Results in the case of the stallions are preliminary, but indicate the same patterns as found in the case of the mares. We conclude that the free-ranging equids in the present study, both mares and stallions, simply defecate and urinate where they graze. Intensively grazed patches are more fouled compared to less grazed patches, which is in contrast with the patterns described in literature for horses in small pastures (Archer, 1972; Archer, 1973; Ödberg & Francis-Smith, 1976). Grazing and eliminating were not spatially separated in Camargue horses (Sereni, 1977). Similar, Tyler (1972) found no evidence that free-ranging ponies in the New Forest grazed and defecated in separate areas. However, based on their study in unenclosed, improved grasslands in the New Forest, Edwards & Hollis (1982) stated that the establishment of distinct latrine areas by horses does occur in free-ranging animals.

Why seem horses not to concentrate their faeces in non-grazed patches, when grazing in a large, spatially heterogeneous environment, and are consequently faced with faecal droppings in the grazed patches? We suggest that animal density, spatial vegetation heterogeneity and plant productivity of the grazed area could play a role. Also the parasite status of the grazing animals and the grazed areas could have an impact. Probably, animal density, and thus consequently faecal density, is of major importance. Herbivores avoid grazing near faecal droppings (Ödberg & Francis-Smith, 1977; Archer, 1978; Hutchings et al., 1998), which is thought to be an adaptation to reduce infection by intestinal parasites (Taylor, 1954). Many studies of herbivores have shown that the animals select non-contaminated swards, when available, over faeces (from the own or another species) contaminated swards (Marten & Donker, 1964; Forbes & Hodgson, 1985; Hutchings et al., 1998). Hutchings et al. (1998) found a threshold level of faecal contamination of swards for sheep: experimental sward trays with 15 g faeces and above were rejected by the sheep (this equated to 198 g faeces per m?). In the four study areas the overall animal density is low (0.13 – 0.38 large herbivore/ha). A low animal density implies a low parasite density. Therefore it is possible that with the current defecating rate of the total herd the grazing animals are not faced regularly enough with faeces (and thus parasites) to establish a pattern potentially reducing the risk of parasitic infection. However, some areas are more intensively used than others, like the "Pasture" grazed by Shetland ponies and Highland cattle in Westhoek-South. According to our suggestion that latrine behaviour is related to animal density, we would expect that on this particular site the horses would use separate patches to graze and to defecate. However, in this case we also did not find evidence for latrine behaviour. The reduction in herbage intake associated with the fouling from dung appears greatest at intermediate grazing pressures but minimal at either very low or very high grazing pressure (Wilkins & Garwood, 1986). It is difficult to know the animal density on an unenclosed area like the "Pasture", but it could be that grazing pressure was here above a potential upper limit. We assumed the "grazing situation" at the "Pasture", to be similar to the point of departure in the study of Edwards & Hollis (1982). However, they reported that the studied lawns showed a mosaic of latrine areas with taller vegetation and non-latrine areas with shorter vegetation. The ponies grazed mostly in the non-latrine areas, though there was seasonal variation, and the highest levels of dunging were in latrine areas. Edward & Hollis (1982) suggested that the formation of latrine areas is related to high animal densities, which should explain the discrepancies with previous conclusions of Tyler (1972) in the

New Forest. However, according to the difference between the results at "The Pasture" and the results at the New Forest grasslands, we assume that also other factors have to be taken in mind. We suggest that the level of heterogeneity of the grazed area plays a role too. The grasslands considered in the New Forest were rather homogeneous. The above-ground biomass of herbage was higher in the latrine areas and the proportion of some species present varied between latrine and non-latrine areas, however species composition showed rather few differences between the two areas (Edward & Hollis, 1982). Our study site "The Pasture" forms a clear spatial entity within its surroundings but is still heterogeneous on lower spatial levels. Overall the area is "grassy", with several patches of rough vegetation. Within the grassy environment and within the rough vegetation, different vegetation types with specific species composition can be distinguished. Herbivores foraging in heterogeneous environments are expected to be faced with more foraging decisions than when foraging in homogeneous areas. In such situation the avoidance of parasites and thus of faeces may become of minor importance to the decision on grazing where and what. Furthermore, the present study was conducted in nutrient poor systems. It could be that the grazing animals were nutrient-stressed and consequently became less selective, since being selective is time-consuming and thus costly. This latter factor of forage quality can also contribute to the observed differences in eliminative behaviour between horses in pastures and the free-ranging horses of the present study. Domestic animals are mostly 'parked' in pastures with a vegetation cover of a higher nutrient quality compared to the grazed dune areas. Moreover, many domestic horses are fed additional concentrate rations. Thus, the more nutrient-comfort situation of horses in pastures may enable them to display a more selective grazing as well as eliminative behaviour.

An additional explanation for the dissimilarity between our results and those of Edward & Hollis (1982) lays in the 'grazing history'. Ponies have been grazing the New Forest hundreds of years and parasite levels of the intensively grazed lawns may be much higher compared to the parasite levels of the dune reserves with a much younger grazing history. Besides the parasite levels of the grazed area the parasite status of the horses themselves may play a role in the explanation of the lack of appearance of latrine areas. The parasite status and immune status of sheep affects the degree of avoidance of grazing near faeces (Hutchings et al., 1998, 2001a, b, 2002). Immune sheep took higher parasitic risks, while parasitized animals reduced parasitic risk through increased rejection of faeces-contaminated swards and/or changing foraging behaviour. Exposure to internal parasites may lead to a certain degree of immunity in adult horses. They can live with a certain internal parasite load without being harmed seriously. Treatment with an anthelminthic allows an increase in immunity. The equids of the present study could have reached a certain degree of immunity and in addition with the supposed low parasite levels of the grazed areas, the horses may behave like the immune sheep, taking higher parasitic risks. Since no veterinary control of the effective degree of intestinal parasitic infection or of a possible immunity is performed, it is difficult to estimate the possible impact of this factor on the grazing and eliminating behaviour of the studied equids.

Mixed grazing seems to result in a reduced avoidance of faeces contaminated swards (Forbes & Hodgson, 1985). Horses, grazing in combination with other large herbivores, did not perform latrine behaviour (Carson & Wood-Gush, 1983). In the present study two areas were grazed only by equids, in the other two areas the equids were accompanied by Scottish Highland cattle. Since we found similar results in all four cases, we believe that the impact of mixed grazing on the eliminative behaviour of free-ranging equids is of minor importance, given the study site situation. We want to indicate also that herd composition, moreover the sex ratio of the herd, can have far-reaching influences on the behaviour and habitat use of equids.

Our conclusion that horses, grazing in large heterogeneous areas, simply defecate where they graze, has important consequences for nature management. Some studies (Bakker et al., 1983; Putman, 1986; Bokdam & Gleichman, 2000; Bokdam et al., 2001) suggest that there exists a transfer of nutrients in grazed systems, and even more pronounced so in nutrient poor systems. They assume that a depletion of nutrients will occur in the preferred grazing sites, whereas areas with faeces concentration will show an accumulation of nutrients. At this point we can state that this process is not likely to occur on a large scale in nature reserves grazed by equids.

Vegetation types with highest grazing times receive also the highest number of defecations. Thus, nutrients taken by the grazing equids have a great chance to return to these grazed areas, although not necessarily (most probably not) at the very same location.
Another consequence of our findings is that the distribution of faecal pellets in an area gives a fairly good picture of the habitat use of the horses. The faecal-count-method is an indirect method available for trying to assess the patterns of habitat occupancy by secretive wild herbivores (Putman, 1990). According to our results this technique can be valuable to use for free-ranging equids in nature reserves as well.

In the present study we conclude that horses, free-ranging in large heterogeneous areas, do not perform latrine behaviour, as described for horses in pastures. The spatial distribution of the eliminative behaviour could be explained to a high degree by the spatial distribution of the grazing behaviour: horses defecate where they graze. We suggested possible reasons why this behaviour is different with the eliminative behaviour of horses in pastures. Further research is required to investigate the impact of the suggested explanations. Especially experimental set-ups can help to find the answers related to the issue of grazing in relation to faecal distribution.

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Table 4.1.

Animal density in the different areas.

Initial and Final dens.: Equid density at the start and at the end of the observation periods. Total dens.: Animal density (equids and cattle) at the end of the observations. Densities are expressed as number of adult individuals per 10 ha.

Site	Area	Equid breed	Initial dens.	Final dens.	Other large herb.	Total dens.
Westhoek-North	54 ha	Konik horse	0.7	0.9	Highland cattle	1.3
Westhoek-South	60 ha	Shetland pony	1.3	3.2	Highland cattle	3.8
Houtsaegerduinen	80 ha	Donkey	0.7	2.1	-	2.1
Ghyvelde	75 ha	Haflinger horse	2.0	1.6	-	1.6

Table 4.2.

Features of the eliminative behaviour of the equids.

Obs: Number of observation sessions of 6 hours. Mean # per 6 hrs: mean number of defecations/urinations per 6 hours ± standard error. % grazing: the proportion of number of defecations/urinations while grazing over the total number of defecations/urinations. (Note that the different equids were observed for a different amount of 6-hour sessions.)

		Obs	Defecations		Urinations	
		n	mean # per 6 hrs	% grazing	mean # per 6 hrs	% grazing
Mares	Konik horse	18	5.0 ± 0.3	45.6	2.4 ± 0.3	18.2
	Shetland pony	119	3.5 ± 0.2	57.3	2.5 ± 0.2	6.0
	Donkey	169	3.6 ± 0.1	55.0	1.5 ± 0.1	1.2
	Haflinger horse	31	4.2 ± 0.3	59.5	2.9 ± 0.3	23.3
Stallions	Konik horse	33	4.9 ± 0.3	19.8	2.6 ± 0.2	3.5
	Donkey	14	4.9 ± 0.4	7.3	2.3 ± 0.3	0.0

Table 4.3.
Spatial relation between grazing and eliminative behaviour at the vegetation type level.
Correlations between total grazing time in a vegetation type and total number of defecations/urinations or total defecation/urination time in that vegetation type. All variables were square root transformed. n = number of vegetation types. If data were normally distributed the Pearson correlation coefficient was used. If not, we used the Spearman correlation coefficient.

				# Defecations	Defecation Time	# Urinations	Urination Time
Mares	Konik	Graz.time	Pearson r	.901	.864	.836	.839
			p	.000	.000	.000	.000
			n	21	21	21	21
	Shetland pony	Graz.time	Spearman r	.806	.797	.821	.806
			p	.000	.000	.000	.000
			n	92	92	92	92
	Donkey	Graz.time	Spearman r	.835	.825	.719	.705
			p	.000	.000	.000	.000
			n	115	115	115	115
	Haflinger horse	Graz.time	Pearson r	.955	.934	.829	.773
			p	.000	.000	.000	.000
			n	22	22	22	22
Stallions	Konik	Graz.time	Pearson r	.957	.951	.884	.871
			p	.000	.000	.000	.000
			n	22	22	22	22
	Donkey	Graz.time	Spearman r	.460	.457	.500	.511
			p	.000	.000	.000	.000
			n	83	83	83	83

Table 4.4

Spatial relation between grazing and eliminative behaviour at the patch level. a: In the most grazed vegetation types. Only the vegetation types with highest grazing times were considered. b: In a vegetational entity. Correlations between total grazing time in a patch (vegetation type-sward height combination) and the total number of defecations/urinations or the total defecation/urination time in that patch. All variables were square root transformed. n = number of patches. If data were normally distributed the Pearson correlation coefficient was used. If not, we used the Spearman correlation coefficient.

						# Defecations	**Defecation Time**	**# Urinations**	**Urination Time**
a	Mares	Shetland pony	Graz. time	Spearman	r	.780	.789	.710	.703
					p	.000	.000	.000	.000
					n	73	73	73	73
		Donkey	Graz. time	Spearman	r	.655	.636	.457	.439
					p	.000	.000	.000	.000
					n	87	87	87	87
		Haflinger horse	Graz. time	Spearman	r	.909	.884	.797	.774
					p	.000	.000	.000	.000
					n	37	37	37	37
	Stallion	Donkey	Graz. time	Spearman	r	.566	.553	.370	.371
					p	.000	.000	.016	.015
					n	42	42	42	42
b	Mares	Shetland pony	Graz. time	Spearman	r	.781	.772	.648	.633
					p	.000	.000	.000	.000
					n	60	60	60	60

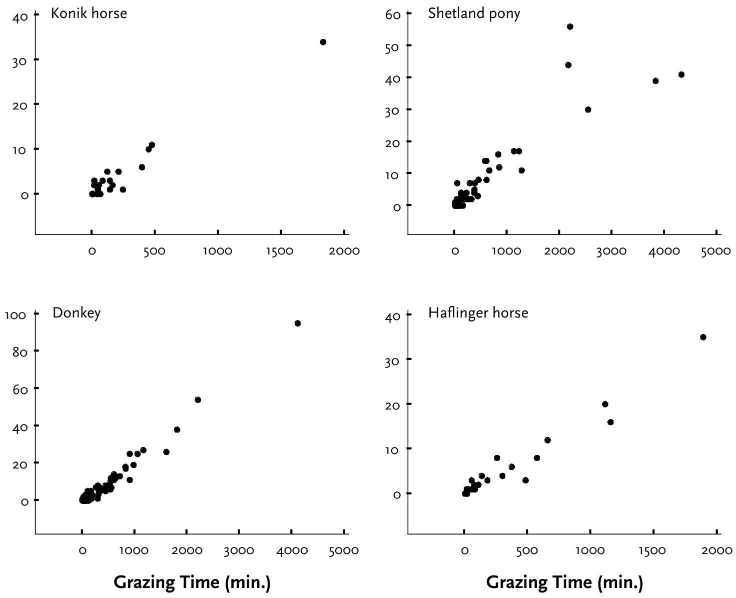

Figure 4.1

Correlation at the vegetation type level for the four mare groups. The total number of defecations in relation to the total grazing time (min.). Every dot represents a vegetation type. See Table 4.3 for the values of r, p and N

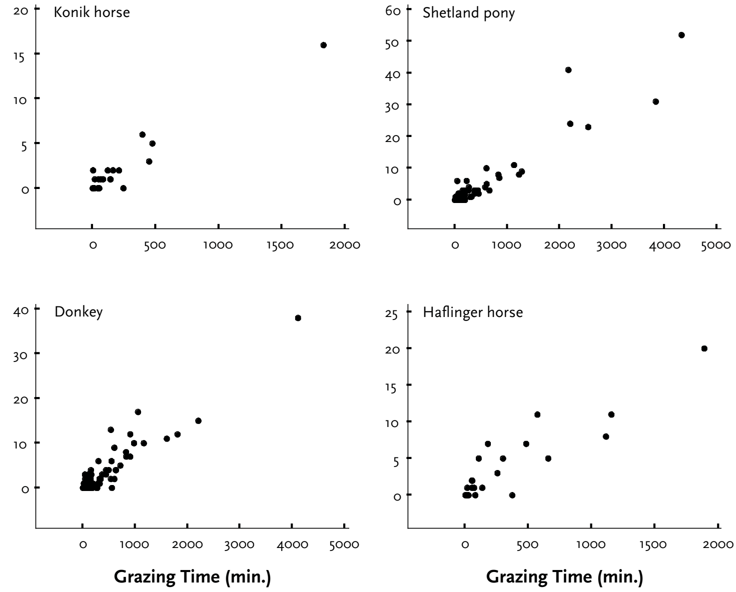

Figure 4.2

Correlation at the vegetation type level for the four mare groups. The total number of urinations in relation to the total grazing time (min.). Every dot represents a vegetation type. See Table 4.3 for the values of r, p and N

5

TIME BUDGET AND HABITAT USE OF FREE-RANGING EQUIDS: A COMPARISON OF SAMPLING METHODS

Lamoot Indra, Callebaut Julie, Demeulenaere Else, Laquière Joy, Hoffmann Maurice

Mutual grooming by two Shetland ponies, Westhoek-South (foto: Indra Lamoot)

Abstract

Do different sampling methods in time budget studies lead to different results? Studies on time budgets or habitat use of animals apply different observation methods. Some researchers use continuous sampling, while most employ instantaneous or scan sampling. Usually no justification is given for the chosen sampling method. In the case of instantaneous or scan sampling the choice of the time interval is hardly ever motivated. It is possible though, that differences in methodology are at least partly responsible for the variation in time budget reported in literature. Therefore, we investigated whether instantaneous sampling with time intervals of 5, 10, 15, 20 or 30 min, respectively, gave the same results as continuous sampling when studying the time budget and habitat use of free-ranging Shetland ponies and donkeys. The data set obtained by continuous sampling is the reference data set. From this data set a new one was derived, representing records sampled every five minutes. This new data set made it possible to calculate the equids' time budget and habitat use simulating instantaneous sampling at time intervals of 5, 10, 15, 20 or 30 min.
The methods of instantaneous sampling with interval 15, 20 and 30 min resulted in time budgets that significantly differed from the time budget estimate based on continuous sampling. Depending on the time interval, we found a significant different proportion of time spent on grazing, walking and 'other behaviour'. These patterns were found for both equid species and all four seasons. On the other hand, all five simulated instantaneous sampling methods gave the same pattern of habitat use as obtained from continuous sampling. Our results show that choosing the correct interval length is important when the researcher selects instantaneous sampling as the observation method. Furthermore, these results suggest that differences in time budget among studies can at least partly be explained by differences in observation methods.

Keywords: equids, time-budget, methodology, observation

Introduction

Recording the behaviour of all individuals of any animal group under study is impossible in field studies and the investigator has to choose a feasible observation method, accurately summarizing all animal behaviour. Hence, the question arises whether there is any standardized methodology for behavioural studies, allowing accurate estimation of true animal behaviour and spatial distribution. Standardization is necessary to avoid wrong or different interpretation due to methodological effects and to make results comparable. Some authors (Gary et al., 1970; Bart et al., 1998) reported the consequences of applying different methods on the validity of conclusions. Already in 1970, Gary et al. (1970) criticized grazing behaviour studies because they lack standardized observation techniques, leading to inconsistent results. Today, more than 30 years later, research on grazing behaviour is still suffering from the lack of a standardized methodology. Altmann (1974) described different sampling methods for field studies on behaviour, with their advantages, disadvantages and abuses. She reported that both focal animal sampling and instantaneous (and scan) sampling are appropriate methods to investigate research questions concerning 'percentage of time'. Instantaneous Sampling is a technique in which the observer records an individual's current activity at pre-selected moments in time throughout the sampling period (e.g. every 10 minutes). Instantaneous Sampling can be used to obtain data from one focal animal or from several individuals, by observing each successively. Scan Sampling is similar to instantaneous sampling by using a time interval to record the behaviour, but here the behaviour of all visible group members is sampled within a very short time period, and hence approaching a simultaneous sample of all individuals. Focal Animal Sampling is a technique in which all occurrences of specified actions of a focal animal and their duration are recorded during a continuous sampling period (Altmann, 1974). Because the method of Instantaneous Sampling can also record the behaviour of a focal individual, we use the term Continuous Sampling in the present study for the Focal Animal Sampling method as described by Altmann (1974).

An animal's time budget represents the proportion of time it invests in different (pre-defined) behavioural types. Habitat (or vegetation) use is defined as the respective proportions of (grazing) time spent in the distin-

guished habitat (or vegetation) types.
Altmann (1974) already stated that most authors only give partial descriptions of the used sampling procedures and, moreover, they rarely provide justification for the choice of sampling method. Based on a comparison of literature on time budgets and habitat use of free-ranging equids, we conclude that different authors apply different methods. Some researchers use continuous sampling (Boyd, 1998; King, 2002; Cosyns et al. 2001), most employ instantaneous or scan sampling (Martin-Rosset et al., 1978; Salter & Hudgson, 1979; Duncan, 1985; Mayes & Duncan, 1986; Pratt et al., 1986; Putman et al., 1987; Gordon, 1989; Van Dierendonck et al., 1996; Moehlman, 1998; Fleurance et al., 2001; Vulink, 2001; Boyd & Bandi, 2002; Menard et al., 2002), using intervals of 1, 5, 10, 15, 30 or 120 minutes, respectively. In one occasion both methods were used (Tyler, 1972). In some cases it is not clear which observation method was employed. Some authors refer to Altmann (1974) for their methodology, but most do not provide any reference at all. In most of the above mentioned studies no justification was given for the chosen sampling method either, nor for the choice of time interval in the case of instantaneous or scan sampling. Only van Dierendonck et al. (1996) performed a pilot study to find out the most appropriate time interval.

Variation in time budget among different studies can be caused by several factors. Biotic and abiotic environment, climate, horse breed, herd composition, animal physiology and others have all been invoked to explain observed variation. However, differences in methodology can also lead to different results, as already suggested by Gary et al. (1970) for the behaviour of cattle.
We studied the behaviour and habitat use of large herbivores, free-ranging in coastal nature reserves. Data were collected through continuous focal animal observation. This method was chosen, because we were not only interested in general time budgets and habitat use, but also wanted information on durations, behavioural sequences and behavioural types of a short duration (Lamoot & Hoffmann, 2004; Lamoot et al., 2004). This data set with continuous observations, is very suitable to test whether instantaneous sampling with a given interval length would give the same results as

continuous sampling when investigating time budget and habitat use. From our original data set we derived another data set simulating instantaneous sampling. In the study presented here, we compare continuous sampling and simulated instantaneous sampling at time intervals of 5, 10, 15, 20 or 30 minutes, respectively.

Materials and methods

Study animals and behavioural observations

We performed our study in two nature reserves ("Westhoek" and "Houtsaegerduinen"), located in the coastal dunes of Belgium. These reserves are relatively nutrient poor systems with a spatially heterogeneous landscape. Spatial heterogeneity is primarily driven by geomorphological and vegetation patterns. Domesticated grazers were released for nature management reasons. "Westhoek-South" (ca. 60 ha), a fenced area in the south of the "Westhoek" nature reserve, is grazed by a herd of Shetland ponies and a group of Highland cattle. In the "Houtsaegerduinen" a herd of donkeys graze all over the nature reserve (total area 80 ha). The animals are free-ranging and remain in the area year round. They receive no additional food. Herd compositions are controlled to avoid inbreeding and overgrazing. In both areas the number of equids increased during the observation period (August 1998 – April 2001), mainly due to breeding. In "Westhoek-South", the pony herd developed from one stallion and 7 adult mares with their foals towards 5 stallions, 9 adult mares, 3 two-year-old mares and 2 colt yearlings in spring 2001. In "Houtsaegerduinen" the donkey herd started with one stallion, 5 mares and 3 foals in summer 1998. In April 2001 the herd consisted of 3 stallions, 7 adult mares, 2 two-year-old mares and 3 colt yearlings.

Observational data were collected through continuous focal animal sampling (Altmann, 1974). We chose a six-hour period as observation unit because this was experienced to be a convenient time period during which a single observer could continuously observe a focal animal without loss of concentration. During each six-hour period we continuously monitored the behaviour of a focal individual, chosen at random from a pool of possible study animals before the start of an observation session. We continuously timed (accuracy 1 s) the consecutive behavioural types, as well as the vegetation type in which it was performed. Vegetation type was coded according to Provoost & Hoffmann (1996). This code is primarily based on vegetation physiognomy (forest, scrub, grassland, ...) and on the dominant plant species. The animals were habituated to the presence of humans and could be approached at close range (i.e.1 m) without visible influence on their behaviour.

Data sets and statistics

Per season and per animal species, nine daytime sessions (somewhere between 6.00h and 18.30h) of continuous sampling were randomly selected, resulting in a data set of 72 sampling periods (of six hours). These observational data are from six donkey mares and eight Shetland pony mares. 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).

We discriminated between grazing, resting up, laying down, walking, standing alert, grooming and 'other behaviour' to calculate the time budget. Time budget was defined as the partitioning of time among these behavioural types.

To determine the habitat use, we lumped the different vegetation types distinguished in the field into seven broader vegetation units: 'vegetation with low plant density', 'grassy vegetation', 'grassy vegetation including taller herb species', 'grassy vegetation with shrub invasion', 'rough vegetation with tall grasses and herbs', 'scrub' and 'woodland'. Habitat use was then defined as the partitioning of the total grazing time among the vegetation units per session.

The data set obtained by continuous sampling is the reference data set. From this data set we derived a second data set, representing records of the behaviour and the vegetation type sampled every five minutes. The new data set allowed us to calculate the equids' time budget and habitat use simulating instantaneous sampling at time intervals of 5, 10, 15, 20 and 30 minutes, respectively. To simulate sampling every five minutes we used all the moments of the new data set. To simulate sampling every 10 minutes we used moments 0, 10, 20, 30 and 40. To simulate sampling every 15 minutes we used moments 0, 15, 30 and 45 of the new data set. For sampling every 20 minutes, we used moments 0, 20 and 40. For sampling every 30 minutes we only used the moments 0 and 30. The percentage of time is estimated from the percentage of samples in which a given activity was recorded (Altmann, 1974).

In order to evaluate the five instantaneous sampling methods in comparison with continuous sampling, an analysis of variance was conducted using the mixed procedure of SAS (System V8), including a repeated statement. Fixed factors are Method, Behaviour or Vegetation, Grazer, Season and all their interactions. We included the factors Season and Grazer because we expected differences in the time budgets and habitat use between seasons and between both equid species. A repeated statement was incorporated to account for repeated sampling of the same individuals. Covariance structures were calculated with the autoregressive method, because this structure always provided the best fitting model. Number of degrees of freedom were estimated by the Satterthwaite method. Our main attention went to the interactions Method*Behaviour, Method*Behaviour*Grazer, Method*Behaviour*Season and Method*Behaviour*Grazer*Season. In the case of the analysis of differences in habitat use the relevant interactions were Method*Vegetation, Method*Vegetation*Grazer, Method*Vegetation*Season, Method*Vegetation*Grazer*Season. Since we were not dealing with the question whether the six methods differed from each other, but wanted to know whether any of the five instantaneous sampling methods differed from the reference method, we implemented the contrast statement. The contrast statement was applied for all previously mentioned interactions. Time budget data and habitat use data are proportions and were arc sinus transformed to approach normal distributions and homogeneous variances.

Results

Time budget

Instantaneous sampling by 15 min, 20 min and 30 min intervals resulted in time budgets that differed significantly from that obtained by the reference method (significant contrast effects for the interaction Method*Behaviour; Table 5.1). Sampling by 15 min intervals gave a significantly different proportion of time spent on one behavioural type (grazing), the 20 min interval gave significant differences for two behavioural types (grazing and ‘other behaviour’), the 30 min interval gave differences for three behavioural types (grazing, walking and ‘other behaviour’). Instantaneous sampling every 5 or 10 minutes did not give a significantly different time budget. There were no interactions with equid species nor seasons, as illustrated by the absence of significant contrast effects for the interactions Method*Behaviour*Season*Grazer, Method*Behaviour*Season and Method*Behaviour*Grazer (which were consequently excluded from the final model). The ANOVA results showed that the time budgets were significantly different between the reference method and the sampling methods with the longer time intervals. However, these differences in time budget were relatively small. Table 5.2 shows the time budget for both donkeys and ponies in all four seasons, calculated with the continuous sampling method (the reference method) and each of the five simulated instantaneous sampling methods.

For each of the 36 observation sessions of both species we calculated the difference in the estimated proportion of time spent grazing between the reference method and each of the five instantaneous sampling methods (Table 5.3). Both the mean difference (a measure for accuracy) as well as the standard deviation (a measure for precision), increase with increasing time intervals. The levels of overestimation and underestimation were highest for the 30 min interval and lowest for the 5 min interval, respectively. On one day the estimated proportion of time spent on grazing by the donkeys, using the 30 minutes interval, was 38.5 % lower than the estimate based on continuous sampling. For other behaviours, we noted a similar increase in the standard deviation of the estimates, and hence a reduction of their precision, with increasing sampling time interval (Figure 5.1).

Habitat use

All five methods based on simulated instantaneous sampling yielded comparable estimates of habitat use as the continuous sampling method (Table 5.4), since there were no significant contrast effects for the interaction Method*Vegetation. Similar results were observed for both equid species and for all seasons (no significant contrast effects for the interactions Method*Vegetation*Season*Grazer, Method*Vegetation*Season and Method*Vegetation*Grazer, which were consequently excluded from the final model).

Discussion

Time budget

The results of this paper show that the choice of the interval length in instantaneous sampling procedures may have important implications. The 5 and 10 min intervals gave a time budget comparable to the reference time budget, obtained from continuous sampling. Recording the behaviour every 15, 20 or 30 min was not frequent enough to provide a reliable estimate of time budget. They respectively gave significant differences with the reference method for 1, 2 and 3 out of 7 behavioural types (grazing, grazing + 'other behaviour' and grazing + 'other behaviour' + walking, respectively). When studying time budgets, time intervals in instantaneous sampling methods above 10 min. should therefore be avoided. However, the differences were relatively small (see Table 5.2) and thus the choice of an appropriate sampling method will be influenced by the desired degree of accuracy.

The number of observation days may play an equally important role to achieve a reliable time budget estimate. The standard deviation of the differences increased with increasing time interval. The high number of observation days (n=36 per species) in the present study resulted in a levelling of the mean values, resulting in a smaller and less significant difference with the reference mean. The differences in time budget between methods would probably be more profound with a smaller number of observation days.

From our results we conclude that the used methodology can contribute to the variation in time budgets found in literature. Pratt et al. (1986) found that Shetland ponies in the New Forest grazed for 75% of their time. They compared their findings with grazing time data of Camargue horses, which spent only 55-65% of their time on grazing (Duncan, 1980), and suggested that this difference reflected different foraging requirements. The differences in estimated grazing investment might be due to several factors, among which environmental differences. However, methodological differences between both studies might be part of the explanation too. Scan sampling was used in both studies, though their time intervals differed largely: Duncan (1980) used a 5 min interval and Pratt et al. (1986) used a 2 hrs interval. Our results suggest that a 2 hr time interval is too long to estimate the horses' time budget accurately.

Habitat use

Patterns of habitat use (defined as the proportion of grazing time spent in the different vegetation types) can be estimated without too much error using instantaneous sampling with a time interval of up to 30 min. The resulting habitat use pattern is not less accurate than the one obtained from continuous sampling. However, it should be mentioned that the reliability of the habitat use estimate largely depends on the number of distinguished vegetation types, their relative area, their spatial distribution and the evenness of time distribution between vegetation types. We hypothesize that longer time intervals are acceptable when habitat use is more homogeneous (such as expected in a spatially homogeneous area). In spatially heterogeneous landscapes with low evenness of habitat use, shorter time intervals will be necessary for accurate estimates of habitat selection. The most appropriate time interval will also depend on the intended level of vegetation typology detail. The researcher interested in a detailed description of habitat use, discriminating between vegetation types that differ only in minor characteristics (e.g. grassland with short, medium and high sward) will probably need shorter time intervals between records.

Other reports on methodology

Only a few studies examined the role of the used methodology on the time budget of large herbivores. In a study on cattle behaviour, Petit (1969) concluded that the time interval has to be a function of the behaviour the researcher wants to study. He found that a time interval of 30 minutes was sufficient to estimate the grazing time of cows and a time interval of 20 minutes was needed in the case of calves. A short time interval of max. 5 minutes was needed to estimate nursing time. Furthermore, with an increasing time interval the variances of the results increased, especially for behaviours that do not last long, like nursing. Gary et al. (1970) investigated the observation frequency needed to obtain a complete picture of cattle behaviour during a 24 hr period. Interval length (1 min, 15 min, 30 min and 45 min) had a significant effect on most of the behavioural variables with the exception of grazing time and lying time. They found no differences between 1 min intervals and 15 min intervals for those activities which are of a continuous nature and which are measurable as a duration, with the exception of nocturnal grazing. Hassoun (2002) tested the effect of sampling frequency on the recorded grazing and rumination time of cattle at pasture. Grazing and rumination time were not significantly different among the time intervals used (5, 10, 15 and 20 min). However, he concluded to retain a 10 min interval for further observations, because in some occasion the 15 and 20 min intervals gave large differences for grazing time and to a lesser extent for rumination time compared to the smallest, and therefore most reliable, time interval (i.e. 5 min).
For time budget studies of horses, only two studies mention some methodological aspects (Martin-Rosset et al., 1978; van Dierendonck et al., 1996). Van Dierendonck et al. (1996) tested whether the estimate of time budget differed between a 10 min and a 5 min sampling interval. They concluded that a 10 min interval was sufficient to describe the time budget of the Przewalski horses. Martin-Rosset et al. (1978) determined the relation between time interval, precision of the time budget estimate and the number of sampled mares: they concluded that 1) the shorter your time interval, the less animals you need to observe to reach a predefined precision and 2) the more precise you want the estimate, the more animals you need when using a certain time interval.

Advantages and disadvantages of the different methods

Instantaneous sampling has the advantage of being less tiring and demanding for the observer than continuous sampling. Another advantage is that a prolonged time interval gives the opportunity to collect other data between two records, e.g. data about the animal's bite rate. The disadvantage of instantaneous sampling is that the final data set contains less information than the data set obtained by continuous sampling. Behavioural types that take (very) short durations and only appear infrequently will hardly ever be observed accurately with instantaneous sampling. A researcher who wants to investigate behaviour occurring as discrete events, e.g. defecating, urinating and flehming behaviour, should use continuous sampling. Finally, one is obliged to choose for continuous sampling when interested in behaviour sequences, certainly in the case of behavioural types with a relatively short activity bout.

In continuous sampling the observer records data from one focal animal per sampling session. Every session another animal is chosen (at random) to be the focal animal. To obtain an accurate time budget estimate it is important to sample more individuals (Martin-Rosset et al., 1978), because individual differences may occur. The final data set based on continuous sampling contains only data from a large number of individuals if a large number of sampling sessions has been performed. If time is limited and the number of research animals should be increased, then instantaneous and scan sampling have a clear advantage compared to continuous sampling, because the behaviour of another individual (instantaneous sampling) or group of individuals (scan sampling) can be recorded every new record (e.g. every five minutes). Furthermore, if one wants to examine the differences in time budget between individuals, then continuous sampling is not very suitable, because the differences between observation days may outweigh those between individuals (Martin-Rosset et al., 1978).

Conclusions

We conclude that if a researcher is interested in the general time budget of free-ranging horses, instantaneous sampling with a time interval of up to 10 minutes is as reliable as continuous sampling, given a large number of observation periods and an even distribution of observations between seasons, as used in our example. To investigate habitat use, the time interval between records can be prolonged up to 30 min. Our results suggest that (largely) different observation methods can at least partly explain the variation in time budgets reported in literature. The methodological factor should not be neglected when implying potential explanations for the observed variation among studies.

Before starting any observation on time budget or habitat use, other methodological aspects should be considered as well. For example, the length of the sampling period may also have an influence on time budget and habitat use estimates, and we already mentioned the importance of factors like the number of sampled animals or the number of sampling sessions. However, the importance of these factors are only rarely or only superficially treated in literature as well (Petit, 1969; Gary et al., 1970; Martin-Rosset et al., 1978). Pilot research is needed in any behavioural study to clarify the effect of these different methodological variables.

It seems that a standardized methodology for grazing behaviour studies is not yet at hand and perhaps not possible, since research questions and environmental conditions very much influence the choice. Some advice can be given though.

We suggest to use continuous sampling when interested in detailed information on behavioural types of (very) short duration, like urinating, defecating, mutual grooming, flehming, and when one is interested in behavioural sequences (Lamoot et al. 2004).

If general time budget and/or habitat use are the research objectives, one can choose for scan sampling or instantaneous sampling. Those sampling methods may be preferred above continuous sampling, because they have some advantages: e.g. being less demanding and several animals can be sampled during one sampling moment or session. Since it is important to sample a large number of individual animals to obtain a truthful estimate of the behaviour of the entire herd, this advantage may be the reason to choose for instantaneous or scan sampling. It appears that in the case of equids with the given environmental heterogeneity, the number of observations, the evenness of observation periods and the number of observed animals, the time interval should not exceed 10 minutes when interested in general time budgets, while it can be extended to up to 30 minutes when only interested in habitat use. When the observer wants to use continuous sampling, it is recommended to make behavioural records from several animals in one sampling sessions, for example by switching to another focal animal every hour.

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Table 5.1

Investigation of the time budget. ANOVA results: effects of the fixed factors and interactions on the variable proportion of time, and the contrast effects for the interaction Method*Behaviour. In the final model, the interactions Method*Behaviour*Season*Grazer, Method*Behaviour*Season, Method*Behaviour*Grazer, Method*Grazer and Method*Season were eliminated because the interactions and contrasts were not significant for these interactions.

Effects of fixed factors and interactions

	df Num	df Den	F-value	p-value
Method	5	2368	10.35	< 0.001
Behaviour	6	645	947.83	< 0.001
Season	3	376	1.14	0.333
Grazer	1	287	6.04	0.014
Method*Behaviour	30	2352	0.83	0.728
Behaviour*Season	18	1497	10.37	< 0.001
Behaviour*Grazer	6	1581	44.36	< 0.001
Season*Grazer	3	376	0.14	0.939
Behaviour*Season*Grazer	18	1497	4.20	< 0.001

Contrasts Method*Behaviour

	df Num	df Den	F-value	p-value
method Cont vs 5’ & Grazing	1	2666	1.74	0.187
method Cont vs 5’ & Grooming	1	2674	0.38	0.538
method Cont vs 5’ & Lying	1	2673	0.27	0.603
method Cont vs 5’ & Resting	1	2673	0.38	0.537
method Cont vs 5’ & Standing	1	2672	0.17	0.682
method Cont vs 5’ & Walking	1	2665	0.33	0.564
method Cont vs 5’ & ‘other’	1	2673	0.72	0.397
method Cont vs 10’ & Grazing	1	2927	2.06	0.152
method Cont vs 10’ & Grooming	1	2923	0.01	0.938
method Cont vs 10’ & Lying	1	2923	0.25	0.617
method Cont vs 10’ & Resting	1	2923	1.11	0.293
method Cont vs 10’ & Standing	1	2924	0.10	0.748
method Cont vs 10’ & Walking	1	2927	1.95	0.162
method Cont vs 10’ & ‘other’	1	2923	3.32	0.068
method Cont vs 15’ & Grazing	1	2629	4.83	**0.028**
method Cont vs 15’ & Grooming	1	2590	0.03	0.859
method Cont vs 15’ & Lying	1	2589	0.14	0.705
method Cont vs 15’ & Resting	1	2590	1.57	0.210
method Cont vs 15’ & Standing	1	2593	0.10	0.751
method Cont vs 15’ & Walking	1	2628	3.83	0.051
method Cont vs 15’ & ‘other’	1	2589	2.94	0.087
method Cont vs 20’ & Grazing	1	2210	9.22	**0.002**
method Cont vs 20’ & Grooming	1	2153	0.65	0.419

Contrasts Method*Behaviour

	df Num	df Den	F-value	p-value
method Cont vs 20’ & Lying	1	2149	0.38	0.540
method Cont vs 20’ & Resting	1	2150	0.98	0.323
method Cont vs 20’ & Standing	1	2155	0.08	0.780
method Cont vs 20’ & Walking	1	2215	2.86	0.091
method Cont vs 20’ & ‘other’	1	1847	4.76	**0.030**
method Cont vs 30’ & Grazing	1	1907	6.51	**0.011**
method Cont vs 30’ & Grooming	1	1854	0.05	0.829
method Cont vs 30’ & Lying	1	1848	0.53	0.468
method Cont vs 30’ & Resting	1	1848	2.89	0.089
method Cont vs 30’ & Standing	1	1854	0.01	0.935
method Cont vs 30’ & Walking	1	1905	6.24	**0.013**
method Cont vs 30’ & ‘other’	1	1847	4.76	**0.029**

Table 5.2

Time budget of both donkeys (D) and ponies (P) in every season (Su: Summer, Au: Autumn, Wi: winter, Sp: Spring) calculated on the basis of the reference method (cont) and each of the five instantaneous sampling methods (M5, M10, M15, M20, M30).

			cont		M5		M10		M15		M20		M30	
			avg	SE	avg	SE	avg	SE	avg	SE	avg	SE	avg	SE
D	Grazing	Su	50,8	4,0	52,0	3,9	52,2	3,8	50,9	4,3	55,6	4,4	49,1	4,5
		Au	61,8	3,7	62,8	3,3	60,8	3,7	62,0	4,7	60,5	4,5	57,4	6,9
		Wi	57,5	3,0	59,3	2,9	59,3	2,6	54,2	4,3	61,1	3,7	51,9	5,3
		Sp	67,2	4,6	67,0	4,4	66,4	4,2	65,3	4,5	67,3	5,4	68,5	4,8
	Resting up	Su	15,9	3,8	16,2	3,6	16,7	3,5	17,1	3,7	17,3	3,3	16,7	3,1
		Au	11,0	2,1	10,8	2,1	11,4	2,4	12,0	2,8	11,7	2,8	13,0	3,7
		Wi	22,3	4,0	23,3	4,2	23,1	4,5	26,4	5,2	24,7	4,6	25,9	5,3
		Sp	14,0	4,3	15,0	4,4	15,7	4,6	16,2	4,3	14,2	3,9	15,7	5,5
	Walking	Su	8,8	1,1	7,4	1,1	7,4	1,6	8,3	2,4	6,8	1,8	8,3	3,1
		Au	11,4	0,8	9,4	1,3	10,8	2,1	8,8	3,4	11,1	2,8	12,0	6,4
		Wi	11,8	1,4	9,3	1,4	9,0	2,1	9,7	2,3	6,8	2,0	11,1	3,1
		Sp	7,5	0,8	7,6	0,8	7,1	1,2	7,4	1,5	7,4	1,9	7,4	1,7
	Lying down	Su	10,5	4,0	10,5	4,0	10,2	3,8	9,7	4,1	8,6	3,7	10,2	4,6
		Au	3,7	1,8	3,9	1,9	3,4	1,7	3,2	1,7	3,7	1,9	4,6	2,4
		Wi	0,2	0,2	0,2	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
		Sp	3,6	1,9	3,9	2,1	4,3	2,4	3,2	1,9	4,3	1,8	3,7	2,8
	Standing alert	Su	8,3	2,9	8,2	2,9	7,7	2,9	7,9	3,4	,0	2,9	9,3	4,3
		Au	8,9	2,4	9,1	2,5	11,1	2,7	10,2	3,2	9,9	2,9	13,0	4,4
		Wi	5,2	2,4	5,7	3,0	6,2	3,1	6,0	3,0	5,6	3,2	6,5	4,3
		Sp	2,1	0,7	1,5	0,5	0,9	0,5	1,4	1,0	1,2	0,8	0,0	0,0
	Grooming	Su	3,1	1,2	3,2	1,4	4,3	1,9	4,2	2,1	1,9	1,3	6,5	3,0
		Au	1,9	0,7	2,6	1,4	2,2	1,2	2,3	1,2	2,5	1,9	0,0	0,0
		Wi	1,7	0,6	1,4	0,8	1,2	0,8	2,8	1,6	0,6	0,6	2,8	2,0
		Sp	3,7	0,8	3,2	1,0	3,7	1,2	4,2	1,8	3,7	1,6	2,8	2,0
	Other behaviour	Su	2,7	0,5	2,5	0,8	1,5	0,7	1,9	0,7	1,9	0,9	0,0	0,0
		Au	1,4	0,4	1,4	0,3	0,3	0,3	1,4	0,7	0,6	0,6	0,0	0,0
		Wi	1,4	0,3	0,9	0,4	1,2	0,5	0,9	0,6	1,2	0,8	1,9	1,2
		Sp	2,0	0,5	1,9	0,4	1,9	0,8	2,3	1,0	1,9	0,9	1,9	1,2

P	Grazing	Su	61,0	3,9	60,5	4,2	59,6	4,5	62,0	4,5	61,7	4,7	60,2	4,3
		Au	82,4	2,3	82,4	2,7	82,7	3,1	82,9	3,8	82,7	3,5	85,2	3,3
		Wi	79,9	4,5	80,4	4,4	81,5	3,7	82,4	3,5	84,0	4,7	81,5	2,7
		Sp	75,1	4,4	75,2	4,3	75,0	4,2	76,9	5,4	74,1	4,3	78,7	4,6
	Resting up	Su	22,2	5,4	22,1	5,4	21,6	5,2	22,2	5,6	19,8	5,9	22,2	5,9
		Au	10,3	2,0	10,2	2,2	10,2	2,0	10,2	2,3	9,9	2,4	10,2	2,3
		Wi	13,9	4,0	14,0	4,1	13,6	4,0	12,5	4,0	13,6	4,4	13,0	3,7
		Sp	12,0	3,4	11,3	3,3	11,7	3,1	11,6	4,0	10,5	2,7	13,0	3,7
	Walking	Su	4,9	0,5	5,4	0,7	4,9	1,4	2,8	1,0	6,2	2,0	1,9	1,2
		Au	3,5	0,5	3,4	0,8	2,5	1,3	3,2	0,9	2,5	1,3	1,9	1,2
		Wi	3,0	0,5	2,8	0,9	2,5	1,0	1,9	0,7	1,9	1,3	2,8	1,4
		Sp	4,8	0,5	5,2	0,9	4,9	0,9	3,7	1,1	5,6	1,6	1,9	1,2
	Lying down	Su	2,6	2,0	2,8	2,1	2,8	2,2	2,8	2,3	3,1	2,5	2,8	2,8
		Au	1,3	0,6	1,2	0,5	1,2	0,7	1,4	0,7	1,2	0,8	0,9	0,9
		Wi	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
		Sp	1,3	1,0	1,4	1,1	1,5	1,2	1,9	1,4	1,2	1,2	1,9	1,9
	Standing alert	Su	5,8	2,5	5,9	2,5	7,1	2,7	6,9	3,0	7,4	3,5	8,3	3,7
		Au	1,2	0,3	1,1	0,4	1,5	0,7	0,9	0,6	1,2	0,8	0,9	0,9
		Wi	1,7	0,8	1,5	0,8	1,9	0,9	1,9	1,0	0,6	0,6	1,9	1,2
		Sp	2,4	0,6	2,3	0,6	2,5	0,7	2,3	1,0	2,5	1,0	2,8	1,4
	Grooming	Su	1,2	0,5	0,9	0,5	0,9	0,5	0,9	0,6	0,0	0,0	1,9	1,2
		Au	0,4	0,2	0,6	0,5	0,6	0,4	0,5	0,5	1,2	0,8	0,0	0,0
		Wi	0,7	0,4	0,5	0,3	0,3	0,3	0,5	0,5	0,0	0,0	0,0	0,0
		Sp	1,9	0,9	2,3	1,1	2,8	1,2	2,8	1,8	3,7	2,1	1,9	1,2
	Other behaviour	Su	2,5	0,7	2,5	0,6	3,1	0,6	2,3	1,0	1,9	0,9	2,8	1,4
		Au	0,9	0,2	1,1	0,5	1,2	0,5	0,9	0,9	1,2	0,8	0,9	0,9
		Wi	0,7	0,2	0,8	0,3	0,3	0,3	0,9	0,6	0,0	0,0	0,9	0,9
		Sp	2,6	0,8	2,3	0,8	1,5	0,7	0,9	0,6	2,5	1,3	0,0	0,0

Table 5.3

Precision and accuracy of the tested methods.

Difference in proportion of time spent grazing (%) when using the methods sampling every 5 min. (D5), every 10 min. (D10), every 15 min. (D15), every 20 min. (D20), every 30 min. (D30), compared to the reference method, based on the 36 observation days for both species. Mean: average difference in % grazing for each of the five methods compared to the reference method (N=36). SD: standard deviation. Max underestimation: the largest negative difference found. Max overestimation: the largest positive difference found.

		D5	D10	D15	D20	D30
Donkeys	Mean	0.9	0.3	-1.2	1.8	-2.6
	SD	2.5	4.0	6.7	7.5	12.3
	Max underestimation	-4.8	-6.4	-17.7	-14.0	-38.5
	Max overestimation	6.5	7.9	9.9	17.6	15.6
Ponies	Mean	-0.0	0.1	1.4	1.0	1.8
	SD	2.0	3.7	5.0	5.0	7.6
	Max underestimation	-5.0	-8.6	-7.8	-11.4	-12.6
	Max overestimation	3.4	7.1	12.2	11.6	18.2

Table 5.4

Habitat use of both donkeys (D) and ponies (P) (averaged over the four seasons) calculated on the basis of the reference method (cont) and each of the five instantaneous sampling methods (M5, M10, M15, M20, M30).

		cont		M5		M10		M15		M20		M30	
		avg	SE	avg	SE	avg	SE	avg	SE	avg	SE	avg	SE
D	Grassy	13,7	5,0	13,5	5,0	14,1	5,2	13,1	4,9	15,4	5,8	13,3	5,4
	Grassy/open	18,3	5,1	18,1	5,4	17,6	5,6	18,2	5,6	16,2	5,5	19,9	6,5
	Grassy/rough	19,9	5,9	19,7	5,8	19,4	6,0	18,8	6,3	18,9	5,9	16,1	6,4
	Grassy/shrub	14,6	4,4	14,7	4,7	14,7	5,2	15,0	4,9	14,0	5,1	17,0	6,3
	Rough	22,1	6,1	22,7	6,3	23,6	6,7	23,1	6,9	23,5	6,6	26,5	8,5
	Scrub	12,1	5,0	12,3	5,2	12,4	5,6	12,1	5,3	12,8	5,9	11,8	6,2
	Wood	12,7	4,1	12,6	4,2	12,0	4,3	13,8	4,6	12,6	4,8	11,7	4,7

		cont		M5		M10		M15		M20		M30	
		avg	SE	avg	SE	avg	SE	avg	SE	avg	SE	avg	SE
P	Grassy	33,8	10,7	33,8	10,6	33,9	10,9	33,7	11,2	33,8	10,8	34,2	11,7
	Grassy/open	3,1	1,8	2,7	1,8	2,7	1,7	2,7	2,0	2,5	1,8	2,7	1,9
	Grassy/rough	14,6	5,1	14,7	5,1	14,6	5,3	14,6	5,4	13,5	5,1	14,1	5,7
	Grassy/shrub	6,9	4,3	7,1	4,4	7,3	4,5	7,1	4,6	8,0	4,9	7,7	4,9
	Rough	28,9	6,1	29,1	6,3	29,1	6,4	28,6	6,4	29,5	6,3	26,8	7,2
	Scrub	7,4	2,6	7,3	2,8	7,0	2,9	7,6	3,1	7,4	3,3	8,2	3,4
	Wood	5,2	3,2	5,4	3,3	5,4	3,4	5,8	3,4	5,2	3,4	6,4	3,9

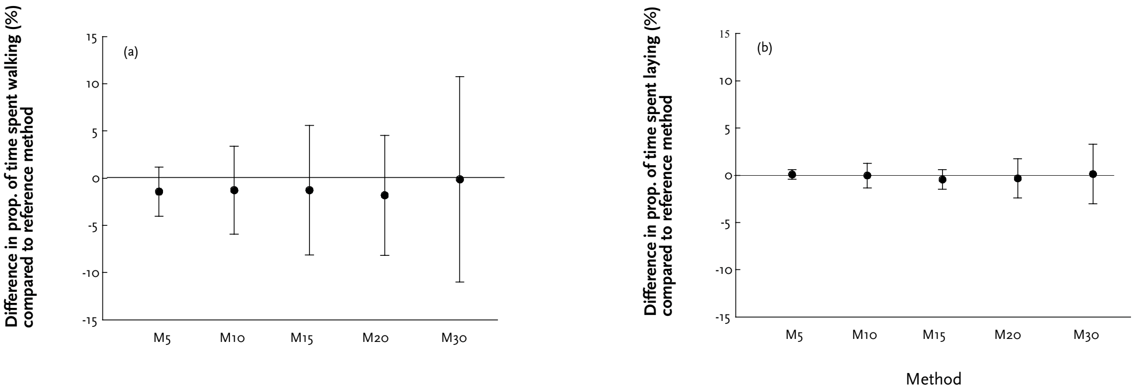

Figure 5.1

Precision and accuracy of the tested methods.

Mean (± SD) difference in % walking (a) and % Lying (b) for each of the five methods compared to the reference method in the case of the donkeys (N=36 observation days).

M5, M10, M15, M20, M30: method with sampling every 5, 10, 15, 20, 30 min, respectively

6

GENERAL DISCUSSION

HERD OF SHETLAND PONIES, WESTHOEK-SOUTH (FOTO: INDRA LAMOOT)

Different species and breeds of large ungulates have been introduced into several dune reserves along the Belgian coast as a management measure. The nature conservation expectations of this grazing management are high. Management results and the predictability of them still carry a high level of uncertainty since little is known about the possible impact of the herbivores on such relatively low-productive, heterogeneous ecosystem. The knowledge about habitat use and dietary choices of different herbivore species in different ecosystems can help to predict the potentially dissimilar impact on vegetation.

The research reported here has sought to gain better insights into the (foraging) behaviour and the habitat use of the large herbivores in such a low-productive environment, with a considerable amount of spatial and temporal heterogeneity. We focused on different herbivore species and breeds, since we expected differences in their foraging behaviour and habitat use, due to their morphological and physiological differences. In the end, the results of the study are expected to contribute directly to the understanding of the herbivore impact.

In this concluding chapter, we want to reassemble our most important findings. After a first characterization in terms of time budget, habitat use and diet composition, considerable attention will be given to species and breed differences in foraging behaviour. Possible mechanisms of foraging at the landscape level are discussed next. Finally, some aspects of the herbivore impact are tackled.

Foraging behaviour and habitat use of large herbivores in coastal dune reserves

Observing large herbivores free-ranging in coastal dune reserves in Belgium revealed that the time-budget of the studied Haflinger horses, Shetland ponies and donkeys is similar to that described in literature for free-ranging horses in other temperate regions (Duncan, 1985; Pratt et al., 1986; Berger et al. 1999; Cosyns et al., 2001; Menard et al. 2002). Grazing is the main activity (56%-71% during daytime; see Table 6.1), followed by resting (12-18%). The Highland cattle we observed spent less time foraging than the equids (38% of their daytime), which is equally in line with other studies (Arnold & Dudzinski, 1978; Arnold, 1984; Menard et al. 2002; Vulink, 2001). In terms of seasonality, it is clear that equids and cattle spend less time grazing in summer than in other seasons. We suggest that this is as an adjustment to the temporal changes in forage quality and quantity. Indeed, grazing time is generally lowest when forage is abundant and of good quality; likewise, it is highest when forage quality is low or forage availability limited (Vallentine, 1990; Stuth, 1991). Haflinger horses, Shetland ponies and Highland cattle had indeed longest grazing times in winter (compared to the grazing time in summer an increase of 39%, 14% and 54% occurred, respectively). Not surprisingly, winter is the season when biomass and quality of the available forage reach very low levels (unpubl. data Cosyns; see Table 1.1-2; Appendix Table A.1-5). Donkeys had also longer grazing times in autumn and winter (an increase of 29% compared to summer), though reached their longest grazing times in spring (an increase of 42%). Total graminoid availability is still very low in spring (comparable to the levels is winter), though live biomass of graminoids is already increasing then, due to the fresh regrowth of graminoids. We suggest that the donkeys' further increase in grazing time in spring is a reaction on this new availability of the sparse, but highly qualitative graminoid shoots. If we assume that the animals have a maximum threshold value for foraging investment (see Duncan, 1992), these figures indicate that the donkeys did not yet reach this threshold value in winter, which might well be the case for both Haflinger horses and Shetland ponies. This was assumed already by Cosyns et al. (2001) for Konik horses in a neighbouring coastal dune area. In gener-

al, the Konik horses spent 73% of their time on grazing without significant grazing time increase in the low productive winter period, suggesting maximum threshold values for grazing for Konik around 70 to 75 %.
Figures on seasonal variation in energy and nutrient requirements are not available, but it might be that large herbivores have higher requirements during the cold season in terms of thermoregulation. Hence, longer grazing times in winter could at least partly be the result of the higher requirements. Equids and cattle have a thicker coat during the cold seasons, but it is possible that this not prevents an increased loss of heat towards the environment then. However, it has also been suggested that cattle have a reduced metabolic rate in winter, resulting in lower maintenance requirements (van Wieren, 1992).

What patterns could be observed in terms of habitat use? Throughout the year, the herbivores foraged in all the distinguished habitat types, but the distribution of foraging activities was not in accordance with habitat availability. This non-random habitat use can be interpreted as a reflection of habitat and diet preferences. Shetland ponies and Highland cattle in Westhoek-South, Haflinger horses in Ghyvelde and donkeys in Houtsaegerduinen all foraged most in the grass-dominated habitat.
When looking at a higher resolution level within the grassy habitat and when taking into account habitat or vegetation unit availability (Table 6.2; Jacobs' index of selection (1974)), we found the following patterns. Haflinger horses preferred grazing in the *Carex arenaria* dominated grassland only. The Highland cattle and Shetland ponies strongly preferred to forage in the grasslands, and to a lesser extent in grassland with scrub invasion. In addition, the Shetland ponies strongly preferred grazing in rough grassland as well. Moss dune and open vegetation and rough vegetation, i.e. the grassy vegetation units with a smaller cover of graminoids, were less grazed by both cattle and ponies. Within the grassy habitat, the donkeys on the other hand showed preference for all five grassy vegetation units without clear differentiation between them. When it comes to foraging in grassy habitat, we may conclude that Highland cattle, Shetland ponies nor donkeys concentrate all their grazing time in grassland in the narrow sense (in Westhoek-South where cattle and ponies graze, this grassland vegetation

unit encloses the vegetation types 'dry dune grassland' and 'moist *Holcus lanatus* grassland'. The latter probably provides the greatest concentration of relatively nutrient rich forage; it is less moist and less productive in the Houtsaegerduinen, where the donkeys forage). However, the donkeys seem to be less selective compared to cattle and ponies, as they prefer grazing in all five grassy vegetation units. This divergence can be an effect of animal species as well as an effect of the spatial organisation of the environment.

We hypothesized that a habitat shift in foraging activity from grassland towards scrub and woodland would occur in autumn and winter, induced by the diminished availability of graminoids of good quality in combination with the small proportion of the area covered by grassy habitat (in Westhoek-South and Houtsaegerduinen). Although there is a decreased grazing pressure in the grass-dominated habitat type in winter in all three areas, the hypothesis was only partly supported by the results. The Haflinger horses did not forage more in woodland or scrub but, surprisingly, increased the use of the moss dunes in which very low biomass figures occur in all seasons (Figure 2.1.2). Ponies and certainly cattle foraged more in scrub in autumn and winter, but only cattle increased their browsing activity in scrub in autumn and winter. The ponies stuck to their diet of mainly graminoids and some forbs when foraging in scrub. In spring, not in autumn and winter, both cattle and ponies increased their foraging time in woodland, foraging a lot on forbs in addition to graminoids (Figure 2.2.1). The donkeys indeed intensified the use of scrub and/or woodland in autumn and winter compared to summer and spring, although we found a variable use of scrub and woodland during the three year observation period. In 1998 the donkeys foraged more in woodland in the seasons with lowest biomass production, while in the autumn and winter of 1999, and especially of 2000 they shifted to scrub. The donkeys even grazed as much in scrub as in the grassy habitat in winter 2000 (Figure 2.3.1). Summarizing, donkeys and cattle are the herbivores showing the greatest habitat shift in autumn and winter, and hence confirming our expectations the most.

When it comes to diet composition of the herbivores, we found that the Shetland ponies and Highland cattle in Westhoek-South and the donkeys in the Houtsaegerduinen are true grazers with a diet consisting mainly of graminoids (Table 6.1). This is in line with previous studies on cattle and horses in various ecosystems (Olsen & Hansen, 1977; Van Dyne et al., 1980; Hanley & Hanley, 1982; Krysl et al., 1984; Vulink, 2001; Menard et al. 2002). Yet diet composition is also largely influenced by season and foraged habitat type (Table 2.2.6, Table 2.3.5). On top of that, from the observations on diet composition of the donkeys from two subsequent years, we could further conclude that their diet composition - like their habitat use - also appeared to be highly flexible over a longer time period (Table 2.3.5). We expected a greater diet divergence between ponies and cattle, but this was only partly confirmed by our results. In general, cattle browsed more than ponies, while ponies hardly ever consumed woody plants. In summer and autumn, cattle also consumed more forbs than the ponies did. In winter the ponies foraged more on forbs than the cattle, which browsed more in that season. However, when grazing in grassland cattle and ponies had a very similar diet composition.

Moehlman (1998a) reported that the donkey has the dentition for grazing, though appears also to have special adaptations for browsing. Some studies reported browsing activity of donkeys foraging in an arid environment (Aganga & Tsopito, 1998; Moehlman, 1998b). Therefore, it was expected that donkeys would browse more than other horses. As mentioned above, the donkeys in our study acted as true grazers, with a diet of mainly graminoids. However, 9% of the bites taken per day were from woody plants, which is more than in the case of the Highland cattle and Shetland ponies in Westhoek- South (Table 6.1). Browsing activity of the donkeys was highest when foraging in scrub (to 14-25% of their diet; Table 2.3.5).

Data all together suggest that, whatever season, all studied animals prefer grassy habitat for foraging as long as plenty of graminoid food is available. Only shortage of this food item, in combination with a low quality, forces them to forage in scrub or woodland. If possible they mainly remain on a graminoid diet in these woody habitats, besides an increased use of forbs. This is most marked for Shetland ponies, and less for Highland cattle and donkey, which appear to show at least some attraction to browse.

So far, we only described habitat use in terms of grazing behaviour. Now we also want to discuss habitat use in relation to eliminative behaviour. Studies on habitat use of free-ranging herbivores rarely discuss eliminative behaviour. Horses grazing in pastures concentrate their faeces in latrine areas where they do not graze (Archer, 1972; Archer, 1973; Ödberg & Francis-Smith, 1976). Little information is known about these fouling patterns in large and spatially heterogeneous areas, reporting contrasting results. Most authors mention the issue only indirectly, though one study (Edwards & Hollis, 1982) investigated it thoroughly. Tyler (1972) found no evidence that ponies in the New Forest, grazed and defecated in separate areas. Moehlman (1998a) stated that, in contrast with donkey stallions, female donkeys of all ages showed little interest in dung and simply defecated where they stood. In contrast, Edwards & Hollis (1982) found that the ponies foraging an area of grasslands in the New Forest established latrine areas, where they avoided grazing.

On the basis of our observations, we conclude that free-ranging equids in large heterogeneous areas do not perform latrine behaviour, but defecate where they graze. In all four coastal dune areas, each grazed by another equine breed or species, we found that the spatial distribution of the eliminative behaviour could be largely explained by the spatial distribution of the grazing behaviour. Active avoidance of the faeces while grazing was also not observed. Moreover, we have seen a few times young foals consuming fresh fecal material (i.e. coprophagy, which is not uncommon in foals (Waring, 2003)). Possibly, animal density is of major importance to explain this behavioural difference with horses in pastures (Archer, 1972; Archer, 1973; Ödberg & Francis-Smith, 1976). Yet spatial vegetation heterogeneity and plant productivity of the grazed area, as well as parasite status of the grazing animals, may also play a role. The conclusion that free-ranging equids defecate where they graze has important consequences for nature management, which we will discuss further on.

Foraging behaviour: differences between herbivore types, animal species and breeds

Put different herbivore species or breeds in a certain living area and they will use this area differently. The specific use of the area is the outcome of the differences in behaviour of the large herbivores. Most important are the differences in foraging behaviour since foraging is the main activity. The variation in foraging behaviour is partly due to differences in nutritional requirements among the respective species, breeds and even individual animals. The variation in nutritional demands is in turn due to intrinsic factors, like metabolic rate, digestive system, body size, reproductive state, age, etc. Other intrinsic factors affecting the variation in foraging behaviour include mouth morphology, historical background and health condition. The interest in herbivore comparisons is often inspired by questions about grazing management as a means for nature conservation. It is recognized that different herbivore species may cause widely dissimilar impacts on the vegetation, but methodological obstacles have hampered the accumulation of insight in this domain (Bakker, 1998). Since there is still no clear consensus about the effect of herbivore species on the biodiversity of grasslands (Rook et al. 2004) as well as other ecosystems (Bakker, 1998), the knowledge about habitat use and dietary choices of different herbivore types in different ecosystems can help to predict the potentially dissimilar impact on vegetation. This knowledge may also help to choose the adequate herbivore type in terms of the desired nature conservation objectives.

Cattle versus equid foraging behaviour

Cattle and equids differ in many respects, though the difference in digestive system and its consequences is probably the most striking one. As ruminants, cattle deal in a totally different way with ingested food than hindgut fermenters, like equids (see Chapter 1). The advantages and disadvantages of both systems can be summarized as follows: ruminants have a higher digestion efficiency of fibrous food than equids, but they have a restricted intake rate due to the time-consuming digestion process. Equids digest their forage less thoroughly than cattle. However, they have a shorter retention time than cattle allowing them to compensate the lower digestion level with higher intake rates. It has been suggested that ruminants are able to extract more nutrients per day when feeding on medium quality forages, while on very high as well as on low fibre forages equids would achieve a higher nutrient extraction per day ('nutritional model': Bell, 1971; Janis, 1976; Foose, 1982). However, several more recent studies have revealed that equids are capable of extracting more nutrients per day on all forages (Duncan et al., 1990; Menard et al. 2002). Illius & Gordon (1992) reported that the more efficient digestion by ruminants is only advantageous over the equids' system when food quantity is limited and food intake is restricted, since ruminants require 20% less food to obtain the same energy yield compared to equids of similar body size. Duncan et al. (1990) suggested that the ability of the rumen flora to detoxify plant secondary compounds may be a more important advantage of ruminants over equids. It is recognized that secondary plant compounds play an important role in the interaction between herbivores and their forage.

Next to physiological differences, also morphological differences such as body size and mouth morphology may affect foraging behaviour of cattle and equids. In absolute terms, larger animals have higher nutritional demands than smaller animals. However, smaller animals need more energy per unit body weight than larger animals, since energy requirements scale with body mass to the power of 0.75, while gut capacity is isometric to body mass (Demment & Van Soest, 1985; Illius & Gordon, 1987). When comparing cattle and equids, we expect though that physiological differences will be more important than body size related consequences.

Mouth morphology of cattle and horses shows remarkable differences, resulting in an adjusted foraging behaviour. While horses cut the vegetation with their two rows of incisors, cattle miss the upper incisors and have to pull off the forage with their large tongue. As a consequence, horses are able to graze on very short sward heights, while cattle are said to be constrained in short sward vegetation (Illius & Gordon, 1987). Furthermore, it is often thought that the absence of upper incisors prevents cattle from foraging as selectively as equids do. The fact that equids need to consume larger quantities of food is more or less in contrast with this assumed higher ability to select certain food particles. A recent study reported that horses

were less selective than cattle in a mixture of soft leaves and stiff stems. Therefore, the authors suggested that the lack of upper incisors in cattle might be advantageous to cattle (Hongo & Akimoto, 2003).
Although cattle and equids differ in e.g. digestive system, mouth morphology and body size, the relationship between differences in those animal specific features and differences in foraging behaviour are often ambiguous. Why ruminants and hindgut fermenters forage in distinct ways and use their habitats differently remains largely unanswered (Duncan et al. 1990).

Foraging behaviour and habitat use of cattle and equids have been compared in several ecosystems in the temperate region (e.g. New Forest: Pratt et al., 1986; Putman, 1996; Rhum: Gordon, 1989b, 1989c; Gordon & Illius, 1989; Camargue: Menard et al., 2002; Oostvaardersplassen: Vulink, 2001). Comparison within a coastal dune area with its spatial heterogeneity and its low productivity level is done here for the first time.
Using the formulas presented by Menard et al. (2002) we calculated that a Highland cow of 481 kg consumes a quantity of dry matter similar to that consumed by a Shetland pony of only 205 kg (4.7-12.2 and 5.5-11.6 kg dry matter per day, respectively). Thus, despite their much shorter grazing time, cattle removed a similar quantity of biomass per individual as ponies per individual. Since cattle take a much smaller number of bites than the ponies, the former must have a greater bite mass. Differences in habitat use and diet composition will determine the differences in impact on the environment of the two species. Despite the large differences between the ruminant and hindgut digestive system, both the equids' and cattle's specific system are developed to digest large quantities of fibrous food, like graminoids. The Highland cattle and Shetland ponies grazing in the Westhoek indeed consumed mainly graminoids (see Table 6.1), but, as expected, the cattle completed their diet, more than equids, with dicotyledons. In fact, the cattle did not consume more herbaceous dicotyledons, but differentiated from ponies mainly through their larger consumption of woody dicotyledons. The Shetland ponies did not browse, which can be explained as an avoidance of secondary plant compounds as well as an avoidance of high lignin contents. Particle breakdown by chewing facilitates a more efficient digestion of the food (Gordon, 1989c). A high lignin con-

tent slows down the rate of particle breakdown during mastication (Spalinger et al., 1986 cit. in Gordon, 1989c). In cattle this chewing occurs mainly during rumination, but in equids mastication has to occur prior to swallowing. A prolonged mastication time would reduce the intake rate of the ponies.

Since we expected a larger use of dicotyledons by the cattle, we also expected a larger use of scrub and woodland. The results confirmed this hypothesis, with the cattle concentrating their grazing behaviour less in the grass-dominated habitat type than the ponies did. In winter, the cattle grazed as much in scrub as in the grassy habitat and in spring they foraged more in woodland than in the grassy habitat. When foraging in scrub and woodland, they increased the amount of forbs and browse in the diet. Furthermore, we expected that within the preferred grasslands, there would occur a differentiation in the sward heights used by the two ungulates, this was indeed the case. The ponies grazed more often in the very short swards than the cattle. This was also concluded by Menard et al. (2002) for (salt) marsh and natural and old field grasslands. It is not clear whether the cattle were morphologically constrained to graze short swards through the lack of the upper incisors, since they achieved high bite rates on the short swards. Probably, cattle foraged less in the short swards, because they are restricted in their effort to consume enough biomass within a limited grazing time.

Beside determinants such as digestive physiology, body weight and mouth morphology, we suggest that additional mechanisms contribute to the differences in foraging behaviour between cattle and horses. The way both species deal with the presence of natural barriers may be one of them. To the ponies, dense scrub is much more of a boundary than it is to Highland cattle. The cattle's wide horns seem to facilitate moving through dense scrub. In addition, cattle may be more explorative than ponies, as we found that the habitat use on the landscape level (Senft et al.1987) was broader for cattle than for ponies.

Differences in foraging behaviour among equids

Questions on the foraging differences between cattle and equids are frequently treated in literature (e.g. Duncan et al., 1990; Clauss et al., 2003) and at least some have also dealt with the issue in a free-ranging situation (e.g. Pratt et al., 1986; Gordon, 1989b, 1989c; Gordon & Illius, 1989; Putman, 1996; Vulink, 2001; Menard et al., 2002). Only recently it has been put forward that differences in foraging behaviour may even occur between breeds (Rook & Tallowin, 2003; Rook et al. 2004). Some aspects of behavioural differences between breeds have been investigated for cattle (see Rook et al., 2004: D'hour et al., 1994; WallisDeVries, 1994; Cid et al., 1997; Berry et al., 2003) and sheep (see Rook et al., 2004: Newborn et al. 1993; Du Toit & Blom, 1995; Du Toit, 1998). However, no thorough research has ever been performed on the variation in foraging behaviour between different free-ranging equid breeds or even different equid species.

The domesticated donkey, a breed belonging to the species *Equus asinus*, and the Shetland pony and Haflinger horse, both breeds belonging to the species *Equus caballus*, are only a few of the numerous equid breeds. Donkey and Haflinger horse are rather rarely used in nature management, though many other horse breeds are (Cosyns & Hoffmann, 2004). A few studies have investigated physiological differences between several equid breeds and species (Izraely et al., 1989; Cuddeford et al., 1995; Pearson et al., 2001). Cuddeford et al. (1995) compared digestive efficiency among Thoroughbreds, Highland ponies, Shetland ponies and donkeys. It was found that donkeys retained their food longer in the digestive tract and digested fibre more efficiently than other equids. In that sense, donkeys were more 'ruminant-like'. The donkey appeared also to be the most successful equid in terms of digesting fibre on low protein diets and this may be because it has the best developed mechanism for nitrogen recycling to the hind gut. The experiments of Pearson et al. (2001) confirmed that compared to ponies, donkeys had longer retention times and a higher digestibility of dry matter, energy, crude protein and fibre fractions. They also found that donkeys consumed less dry matter per unit metabolic body weight than ponies, when fed ad libitum. Since voluntary food consumption is proportional to metabolic rate (Kleiber, 1961; Webster, 1985), this may illustrate that donkeys have a lower metabolic rate, and hence lower maintenance requirements than the ponies. The true energy and nutrient requirements of the donkey are unknown. Therefore, they are often assumed to be similar to those of the pony, probably leading to an overestimation (Pearson et al. 2001). These differences in requirements and digestive abilities between equid species can lead to differences in foraging behaviour in a free-ranging situation. Minute adaptive differences between otherwise very similar equid species in north-east Africa (*Equus africanus, E. grefyi and E. burchalli*) have been suggested to allow for different environmental tolerances in the native habitat range (Bauer et al., 1994).

We found shorter grazing times for donkeys than for Haflinger horses and Shetland ponies (Table 6.1). If we assume that all the studied equid groups fulfil their nutritional demands within the used grazing time, we can conclude that donkeys just need less foraging time to meet their needs. The number of bites consumed per day is also smallest in donkeys (Table 6.1). Theoretically the possibility exists that donkeys take larger bites (this was not investigated), but mouth morphology does not give any clue into that direction. More probably, the donkey's lower requirements per unit body weight combined with a higher digestive efficiency are responsible for a smaller investment in foraging time. On the other hand, their longer retention time may also limit the time spent grazing. Data on absolute differences in bite mass when consuming similar forages are lacking, not enabling us to proof or disproof differences in biomass removal. However, based on the data on voluntary consumption (Pearson et al. 2001), the higher digestive efficiency (Cuddeford et al., 1995; Pearson et al., 2001) and the assumed lower basal metabolic rate, we hypothesize that the free-ranging donkeys in the Houtsaegerduinen remove less biomass per kg body weight than the ponies do in Westhoek-South.

The high digestive capacities of donkeys, also on low protein diets (digestibility of a diet is positively correlated with its protein content (van Wieren, 1987)), enables them to forage on graminoids with a high fibre and low protein content. Hence, they do not have to select high quality grasses. This could explain why donkeys not only prefer grazing in the grasslands (which are assumed to offer the highest concentration on relatively good quality grasses), but also in other vegetation units within the grassy habitat such as moss dunes and open vegetation (which are often avoided by Highland cattle and Shetland ponies) (Table 6.2). In these poorer habitats, they consumed large amounts of *Festuca juncifolia* and *Carex arenaria*. Despite the high fibre and low protein content of *F. juncifolia* (high %NDF and %ADF, low %CP; Table A.5, Appendix), it made up 15% of the donkeys' bites in 2001. This may indicate that donkeys are less determined by the need for a high quality diet and might be more 'free' in their foraging choices, resulting in a broader habitat use, compared to neighbouring Shetland ponies and Haflinger horses. However, the broader habitat use may also be the result of the characteristics of the environment, a point that will be discussed further on.

Moehlman (1998a) suggested that donkeys are able to perform more browsing activity than other equids, thanks to their specific mouth morphology. The narrow mouth and mobile lips would enable them to select only the best parts. The diet composition of feral donkeys has not been studied in detail so far (Bauer et al. 1994). Our data on diet composition indicate that donkeys do browse more than Shetland ponies, and maybe even more than Highland cattle. It is possible that donkeys chew their food items more intensively before swallowing than other equids in order to better overcome the negative effect of the high lignin content of browse on digestive capacities. Comparative studies on chewing behaviour are not available, but Mueller et al. (1998) measured the chewing behaviour of the donkeys and concluded that the donkeys chewed for a longer time and made more chewing movements per quantity of food than horses did. When it comes to the higher browsing activity of the donkeys, this difference in chewing behaviour with other equids may ultimately be more important than the greater selectivity permitted by their mouth morphology. Furthermore, increased mastication on a certain food quantity may decrease the prehension rate. We found smaller bite rates for donkeys than for Shetland ponies or Highland cattle (Table 6.1). Also the bite rate of the Konik horses grazing in Westhoek-North was greater than the bite rate of the donkeys in Houtsaegerduinen (Cosyns et al., 2001).

To our knowledge, the present study is the first extensive report on donkey foraging behaviour in a cool temperate region . The results highlight possible differences in foraging time, habitat use, diet composition and biomass removal with breeds of *Equus caballus,* that have been studied in neighbouring coastal dune areas. This assumption is strengthened by the few studies on physiological differences between donkeys, horses and ponies. Veterinary research is needed to provide correct information on the energy and nutrient requirements of the various, free-ranging, equids in (semi-)natural environments. We have very good reasons to believe that the donkey is a suitable animal to play a role in grazing management, especially in low productive, nutrient poor ecosystems. The donkey, with its higher digestive efficiency, would have an advantage, like the ruminant, over the pony or horse where (or when) food resources are limited (Cuddeford et al., 1995). Hence, if one wants to implement grazing as a management measure in an ecosystem with at least a temporarily limited food supply, the donkey may be a better choice than ponies or horses. Further scientific (experimental) confirmation is needed, but it seems at least that donkeys browse more than other equid species. If grazing management seeks to limit the further increase of certain edible woody plant species, the donkey may be an option. However, it should be taken into account that the donkey consumes less dry matter per unit body mass than the pony (Pearson et al., 2001), so more donkey individuals would be needed to remove the same amount of biomass.

The Haflinger horse and the Shetland pony are both breeds of *Equus caballus*. Both breeds had comparable, long grazing times and concentrated their grazing time clearly in the grassy habitat, but the concentration on the grassy habitat was stronger for the Haflinger horsers than for the Shetland ponies (Table 6.1). We found similar patterns when comparing the selection and avoidance of vegetation units of both breeds. They selected the grasslands (in the broad sense of the word) and avoided scrub and woodland. However, Haflinger horses strongly avoided rough vegetation, while Shetland ponies nor selected nor avoided this vegetation unit (Table 6.2). Roughly spoking, both breeds of *Equus caballus* seem to have more similarities in their foraging behaviour and habitat use than compared to the donkey (*Equus asinus)*. However, the comparison of both breeds of *Equus caballus,* like the comparison of *Equus cabalus* with *Equus asinus*, is preliminary, because both breeds are foraging in different areas with differences in spatial configuration, vegetation composition, forage availability and hydrological conditions.

Some remarks on the relation between body weight and foraging behaviour within equids

We want to come back on the relation between foraging behaviour and body size. Irrespective of the digestive system, smaller animals have relatively larger energy requirements than larger animals (Demment & Van Soest, 1985; Illius & Gordon, 1987). Larger animals are able to use forage of lower quality than smaller animals (Demment & Van Soest, 1985). Smaller animals with smaller mouth parts are able to forage more selectively than large animals (Illius & Gordon, 1999). Recent research revealed that grazing time is negatively related to body mass in temperate ruminants (range of body mass: 20-330 kg) (Mysterud, 1998; Pérez-Barberia & Gordon, 1999). Larger species can store more fat reserves to overcome periods of scarcity (Mysterud et al., 2001) and are thus less limited by food availability. The donkey is the smallest of the three equid groups that we studied, though does not appear to fit into the body size related concepts described above. Compared to the other equids, donkeys have most likely smaller relative and absolute energy requirements. In our study, the donkey had lowest grazing times and seemed to be able to digest forage of very low quality. The Somali donkey can tolerate a loss of 30% of its body weight in order to survive in nutritionally extremely poor environments (Maloiy & Boarer, 1971, cit. in Bauer et al., 1994). From all equid species, the donkey stands out in its capacity to cope with low food quantity and quality. These considerations suggest that the impact of body size on foraging behaviour may be overrated in some cases. Other subtle distinctions in physiological and morphological aspects may be of great importance too, like basal metabolic rate or differences in digestive capacity. As they are not so easily to measure as body size, their role may have been underestimated.

Effect of reproductive state of equids on their foraging behaviour

It is well-documented that reproductive state has an effect on the nutritional requirements, with reproductive animals having higher nutritional needs than non-reproductive animals (NRC, 1989; NRC, 2001). However, there is little knowledge about how (free-ranging) animals adjust their foraging behaviour to meet these higher needs. In a preliminary study, we investigated how lactating pony mares and lactating donkey mares differed in their foraging behaviour and habitat use compared to the non-lactating mares. Results show that in both species lactating animals did not spend more time on grazing but increased bite rate compared to the non-lactating mares. The lactating donkey mares took more bites than the non-lactating mares in grassy vegetation only, while the lactating pony mares took more bites in rough vegetation. Within the grassy and rough vegetation, they took more bites only in patches with a short sward height. In addition, lactating mares took more bites of grasses only and not of forbs or woody plants. The extra grazing effort of the lactating animals was not distributed randomly. Lactating mares invested their extra grazing effort principally into those items that are most grazed by the studied equids in general. Possibly the mares increased bite rate instead of grazing time because of the highly synchronous foraging behaviour in herds of equids (Boyd and Bandi, 2002). This herd characteristic might put a behavioural limit to further increase of individual grazing time by lactating mares. Another hypothesis derives from optimal foraging theory. If we assume that the animals obtain an optimal balance between costs and gains, then the net gains achieved through biting faster are higher than the net gains of an increased grazing time in the lactating animals. Further studies are however needed to test these preliminary hypotheses.

Mechanisms of foraging at the landscape level

Free-ranging herbivores have to make many foraging decisions at different resolution levels. Senft et al. (1987) presented the ecological hierarchy encountered by large herbivores while foraging: regional scale, landscape scale, plant community scale and patch level. The highest level for the herbivores in our study is the landscape scale, because the herbivores forage in relatively small, fenced areas. Foraging decisions at this level are taken to select feeding areas, comprising suitable plant communities. At the level of the plant community decisions involve the selection of feeding patches. Foraging decisions at the patch level are made between feeding stations within the patch, e.g. a certain plant species, an individual plant, a plant part. Above we described habitat use and/or diet composition of Haflinger horses, donkeys, Shetland ponies and Highland cattle in coastal dune reserves. Habitat use is the outcome of decisions made at the upper three levels, diet composition is the outcome of decisions made at all four levels. So far, we did not give much attention to the way the animals use their entire living area, which we call 'terrain use'. Decisions made at the landscape level (and the regional level) determine the terrain use. At the plant community and patch scale the most important factors affecting decision making are related to forage characteristics, such as forage availability, nutritive quality and plant defence (Senft et al., 1987; Baily et al. 1996; WallisDeVries, 1994). Forage availability and quality will also play a role in the decision making at the landscape scale, though many more elements interfere. In what follows we describe several aspects which we believe to be important in the mechanisms of foraging at the landscape level. We did not measure these factors nor their impact in a quantitative way, but these ideas are based on our field observations.

In order to disentangle the relevant mechanisms of foraging at the landscape level, two groups must be considered: elements related to the environment and elements related to the animal. Availability and spatial configuration of preferred vegetation types, location of water, natural and human-made barriers and thus accessibility are environmental determinants. Animal factors are: species, breed or individual specific differences in movement patterns, animal origin and background, and social interactions. In general, those elements do not act on their own, but are mutually related. In areas where the preferred vegetation types, like grasslands, are only sparsely available, the herbivores will need to forage in other, less preferred vegetation types. They will 'stick' less to these vegetation types, as the amount of preferred food items is smaller there. Consequently, they will search for more feeding sites and will also try 'alternative' vegetation types. This results into a broader habitat and terrain use. It has been noted that foraging velocity is faster in areas with small amounts of palatable forage (Bailey et al. 1996). Spatial configuration of the preferred vegetation types is as important as the area covered by it. A large area of grassland will influence the foraging behaviour of the herbivores differently than several small grassy patches with a similar total cover. Spatial configuration will have an impact on terrain use, on habitat use, and on diet composition. A small grassy patch can not 'feed' a herd of animals for a long period, so the herd will start foraging in a neighbouring patch of a less preferred vegetation type or will seek for other grassy patches, located elsewhere in their living area. In an experiment with sheep in a grass-heather mosaic, it was found that sheep foraged on heather only 9% of their grazing time when grassland was available as one large patch. When grassland was provided in 12 small patches within heather vegetation, the proportion of grazing time spent on heather was 43% (Clarke et al., 1995a). The herbivores will probably get to know their living area faster and will sooner discover good alternative feeding sites in areas with limited availability of preferred vegetation types or with a heterogeneous distribution of these vegetation types. In areas with large patches of preferred vegetation types, they will be less forced to become explorative. It has been suggested that large herbivores should not be confronted with the best feeding site when introduced, but should be placed in less favoured sites, so that the animals have to move around to find the more preferable feeding sites. Afterwards, when they already have found good feeding patches, they would visit easier the earlier, less favoured feeding sites.

Stuth (1991) reported that the general optimal foraging range of herbivores lies within the range of 0.8 km distance from a water location. In all our study sites the entire area fells within this range. However, we suggest that the locations of the water sources still play a role in the terrain use, even in areas as small as our study sites. In Westhoek-South, several water pools are located in the very much preferred large grassy feeding area. We suggest that the ponies would not ‘stick’ as much to this location as they do now with no pools around. With pools at larger distances, the ponies would have to regularly leave this grassy entity to drink. They would probably forage on their way to the water pool and in its neighbourhood. Water distribution probably affects less the way donkeys use the terrain, as they are more adapted to arid conditions (Izraely et al. 1994).

Accessibility of the area is another factor influencing the decisions at the landscape scale. Clearly, dense continuous scrub will prevent the animals to move through them to explore other places. In the Houtsaegerduinen some isles with highly preferred food items within scrub vegetation were never used by the donkeys, until a path (for tourists) was created which made them accessible. When rough vegetation and scrub are not too dense, donkeys and ponies will make paths, but they will not do so through a dense vegetation of scrub. Especially at the beginning of their introduction, the donkeys foraged often along the fence around the reserve. As this was the place where a strip of scrub had been cleared (to raise the fence), it gave them an easy path. They explored their living area departing from these artificial strips and other existing paths. On the other hand, the Highland cattle in Westhoek-South did move through and did forage in dense scrub, making it more accessible to the ponies in this way.

This latter point illustrates already that differences between herbivore species in movement patterns influence the foraging mechanisms at the landscape level. Differences can even exist between breeds. The reasons for this diversity are manifold. Movement and exploration patterns, for instance, may vary among breeds and species because of a different origin. Feral donkeys are known to make long travel distances (Denzau & Denzau, 1999). We found that donkeys travelled 917 ± 138 m/6hrs. To compare, ponies and cattle travelled 630 ± 31 m/6hrs and 590 ± 50 m/6hrs, respectively. However, the longer travel distances of donkeys in the present study does not necessarily rely on origin, but might be the result of the spatial configuration of the environment as well. Foraging velocity is most likely faster in areas where good feeding patches are more dispersed over the entire area. In addition to origin, recent experiences may also play a role in the movement patterns. For example, whether the animals grazed in homogeneous pastures or in a heterogeneous scrub-dominated environment prior to introduction, will lead to a different habitat use. Furthermore, animals living in the same area for several years are believed to have a good knowledge of that area. They will develop a kind of spatial memory (Bailey et al., 1996) and will have knowledge about specific food items. This is confirmed by our long-term data on donkeys, that decreased their foraging time from introduction onwards. When for management reasons, a number of animals have to be taken away, it is better to remove the young ones and keep those that are 'resident' since long. Removing the latter would be like throwing knowledge away, which may have far reaching influences on the foraging behaviour of the remaining herd at different ecological hierarchies, especially in complex heterogeneous environments. Compared with experienced animals, naive animals spend more time foraging but ingest less forage; they suffer more from malnutrition and ingestion of toxic plants (Provenza & Balph, 1987, 1988). On the other hand, it is also believed that young, rather than older, animals introduce new foraging and habitat selection behaviours into a herd (Provenza & Balph, 1990). The older herd members may have fallen into habits, leading to a decreased explorative behaviour. In that respect, we want to mention that in Ghyvelde we observed that the herd of Haflinger horses often made the same foraging circuit.

Finally, social interactions can have a major influence on the foraging mechanisms at the landscape scale, even within small herds. In Westhoek-South we observed that the dominant stallion kept his harem more together (in the large grassy entity) during the breeding season than during the rest of the year. In equids, groups of young stallions may prefer foraging far away from the dominant stallion and his harem group in order to avoid encounters. A group of geldings, cast away by the dominant stallion in Westhoek-South, was hardly seen in the large grassland entity, but foraged separately from the main herd. The presence of such a group distributes the grazing impact by the equids more over the entire reserve. This can be of significance for the management of parts of the area less preferred by the main herd.

Herbivore impact on their environment

Grazing management objectives in the coastal dune reserves

In the Westhoek and the Houtsaegerduinen grazing management has been implemented to maintain species-rich, alkaline dune grassland (so-called *Polygalo-Koelerion* within the *Cladonio-Koelerietalia*) (Provoost et al. 2002) and to avoid further growth of the dense scrubs that already cover large parts of both areas. Conservation management concentrates on the prevention of further expansion of dominant, highly competitive graminoids, like *Calamagrostis epigejos* and *Arrhenatherum elatius* and shrub species, such as *Hippophae rhamnoides* and *Ligustrum vulgare*. With the implementation of the grazing management it was expected that the herbivores would decrease the vitality and the abundance 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 vegetation types, formed by the above mentioned dominant species. Conservation management also hoped that some valuable vegetation types that are rather vulnerable to intensive grazing activity, like alkaline moss dunes (so-called *Tortulo-Koelerion* within the *Cladonio-Koelerietalia*), would not lose its dune specific species diversity due to tramling activity.

Grazing impact on different vegetation units

Evidently, plant communities that are exposed to only limited foraging will not be severely influenced 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 grazing, trampling or nutrient addition than others. As ponies, cattle and donkeys have been demonstrated to forage a lot in the grass-dominated habitat, they can be expected to have a relatively strong impact here. Given the vegetation selection within the grassy habitat, not all distinguished grassy vegetation units receive a similar grazing pressure. Of course, the relative area taken by the different vegetation types equally influences the grazing impact on each of them. Grassland, foraged intensively by Shetland ponies and Highland cattle in Westhoek-south, takes a relatively small part of the total area only, so that the grazing pressure per hectare is very high, while other grassy vegetation units are exposed to much lower grazing pressures (Table 6.3). In Houtsaegerduinen, the situation is a bit different and varies by year. In 1998 the highest grazing pressure per hectare was found in the open vegetation and moss dunes, grassland and rough grassland. In 2000 the rough vegetation received the highest grazing pressure per hectare (Table 6.3). Of course, not every square meter of a certain vegetation unit is receiving the same grazing pressure. Some patches will be grazed more often than others, and, depending on the degree of isolation, there will also be ungrazed patches, even in highly preferred vegetations.

Moss dunes are thought to be a very fragile habitat type with regards to large herbivore grazing and trampling. In the Westhoek, these moss dunes (considered together with open vegetation) were not intensively used by ponies and cattle. Cattle foraged in moss dunes in winter only, ponies in winter and spring. Donkeys in the Houtsaegerduinen grazed more often in the moss dunes. However, 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 the paths. Therefore, we assume that in all study areas the grazing activity is not a threat to the moss dunes.

Horses like to roll to rub their back and preferred rolling sites are generally places with dry fine soil (Waring, 2003). This was also observed in our study areas. The equids do not roll on bare soil only, but their preferred sites were indeed patches of bare soil. It is possible that some particular sites are free of vegetation as a result of the frequent rolling activity of the equids on this sites. In addition, the rolling behaviour may keep open some areas with sparse vegetation. At the contrary, we suggest that the ‘normal’ walking behaviour of the herbivores will not result in keeping open sparsely vegetated areas, with the exception of paths.

To predict the herbivore impact, it is not only important to ask ‘where do they graze?’, but also ‘what do they eat?’. *Calamagrostis epigejos* is a dominant, graminoid species that is considered problematic so that conservation management aims to prevent its further expansion. Diet composition data 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. As the species is known to suffer from cutting and grazing, we can expect on the basis of our diet data that this species will diminish over time. The development of species-poor grassland dominated by *C. epigejos* (called rough grassland here) after four years of grazing management has been studied in Houtsaegerduinen and Westhoek-South (Vervaet, 2002). Between 1998 and 2001, the grazed plots showed a significantly decreased cover of *C. epigejos* and a significant increased number of plant species. The ungrazed control plots showed a significantly increased cover of *C. epigejos* over the same period, without significant change in number of plant species. Thus, the herbivores seem to be truly suitable to decrease the dominance of *C. epigejos* in the rough grasslands. A similar decrease in cover by *C. epigejos* was also found in Meijendel, a dune area in the Netherlands, grazed by horses and cattle (de Bonte et al., 1999).

Scrub and woodland cover very large surfaces of the coastal dune reserves we studied. Although cattle, ponies and donkeys grazed for a considerable time in these habitats, the grazing pressure remained very small (Table 6.3). The cattle grazed almost as long in scrub (33.3 min./6hrs) as in grassland (39.3 min./6 hrs), but the grazing pressure of cattle per ha scrub (1.34 min./6hrs/ha) was much lower than per ha grassland (7.02 min./6hrs/ha). The same can be concluded for donkeys. Although they spent 16-27% of their daily grazing time in scrub, the grazing pressure per ha scrub is minimal (0.67-0.91 min./6hrs/ha). Donkeys mostly do not move through dense scrub, their grazing activity will therefore often be limited to the edges of the scrub.

Clearly, the Shetland ponies will probably not have any influence on scrub encroachment, since they do not consume woody plants, not even when foraging in scrub. Cattle and donkeys performed browsing activity when foraging in scrub. In winter, Highland cattle and donkeys (in 2001) spent half of their grazing time in scrub (70 min/6 hrs and 95 min/6 hrs respectively). These long grazing times in combination with the browsing activity indicate that cattle and donkeys can have a tempering effect on scrub encroach-

ment. Scrub enlargement of *Ligustrum vulgare* and *Salix repens* is restrained, at least locally, by the browsing activities of donkeys and cattle, respectively. 3.69% of the total number of bites taken by the donkeys in 2001 were from *Ligustrum vulgare*, while 1.32% of the total number of bites taken by cattle were from *Salix repens*. We have no data on bite mass, but it is plausible that a bite of *L. vulgare* is bigger than a bite of some graminoids (like *Festuca juncifolia*), so that these woody species may form an even larger proportion of the total diet. *Hippophae rhamnoides*, which is considered as a problematic invasive shrub species, is browsed now and then by cattle. The *H. rhamnoides* berries are only occasionally consumed by donkeys. Hence, in Houtsaegerduinen, the sole introduction of donkeys will not be sufficient to avoid further encroachment of *H. rhamnoides*, as also suggested for other dune areas grazed by horses (van Breukelen et al., 2002).
The potential impact of cattle on scrub vegetation comes not only from direct consumption, but also from their movements. As a consequence of their large body size and wide horns Highland cattle open up the closed scrub vegetation. It has been observed that individual shrubs were partly damaged by cattle when moving through a scrub vegetation.

Distribution of grazing pressure at the landscape level

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 almost never visited. Consequently, some sites experience a high grazing pressure and are thus intensively 'managed' by the herbivores, while others receive less or no 'management'. In the Westhoek, foraging behaviour of the cattle was more distributed over the entire fenced area, while the foraging behaviour of the ponies was more concentrated on particular zones (see Maps A.5-6, Appendix). One central grass-dominated entity in the Westhoek counted 27.8% of the cattle locations and 54.3% of the pony locations.
Consequently, the impact of grazing by cattle will be more dispersed, while the grazing pressure of ponies will be more aggregated. Vulink (2001) found that Konik horses concentrated on short grassland for most of the

year and cattle foraged more evenly all over the available space (Oostvaardersplassen, the Netherlands). If ponies were the only large herbivores in the Westhoek, it would be very probable that smaller grass-dominated patches would never be foraged at all. Competitive grass and shrub species could thus invade these patches. Although the terrain use of donkeys in the Houtsaegerduinen is not concentrated at one specific site, some parts of the area witness a higher grazing pressure than others (see Map A.7). Closed scrub covers large parts of the reserve in which donkeys, like ponies, do not forage or move through. Grass-dominated islands within these scrubs are consequently never reached.

Nutrient transfer and seed dispersal

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 nutrient transfer is found in areas grazed by sheep (Bakker et al., 1983) and cattle (Bokdam & Gleichman, 2000; Bokdam, 2003). According to our observations, 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 like it has been observed in cattle and sheep. Patches with highest grazing pressure will receive a proportional concentration of faeces and urine.

Seed dispersal is another aspect of grazing management with considerable potential for nature conservation. The endozoochorous seed dispersal by large herbivores depends on several steps: seed consumption, travel through the digestive tract, elimination of germinable seeds and deposition on a patch suitable to the plant species (see Cosyns, 2004). Our results of the eliminative behaviour illuminate that vegetation types with a long grazing time have also a higher defecation frequency. This implies that seeds consumed in a grassland patch, have the greatest chance to be eliminated in a grassland patch again, although most likely not at the same location. The dispersal distance is dependent on retention time and the distance travelled during this period. Since the grass-dominated habitat type is preferred for grazing by the equids, it is expectable that plant species of this habitat have a greater chance to be dispersed by endozoochorous seed transport than plant species typical for scrub or woodland. Of course, the whole process will be equally influenced by plant species characteristics (see Cosyns, 2004). Next to endozoochory, mammal herbivores are also potential epizoochorous dispersers. Research on both processes in donkeys in Houtsaegerduinen revealed a large degree of complementarity of both mechanisms (Couvreur et al. 2004). This indicates that both mechanisms together might play an important role in seed dispersal.

Future research

It is hard to make any decisive and statistically relevant statements on absolute differences in foraging behaviour and habitat use among herbivores, if these are foraging in different areas. Although the nature reserves in which our study areas are situated are all coastal dunes, with equal climate conditions, they show significant differences in terms of spatial configuration, vegetation composition, forage availability and hydrological conditions. As mentioned before, the availability but certainly also the spatial distribution of preferred habitat types, greatly influence the habitat use of large herbivore species. In Westhoek-South 44% of the area is covered by grass-dominated habitat, in the Houtsaegerduinen this is only 23%. On top of that, in Westhoek-South there are several larger grassland patches, such as ‘The Pasture’, in which both ponies and cattle forage a lot. In the Houtsaegerduinen, there is no such large grassland patch available, as all grassland patches are small and scattered between scrub or woodland. In line with Clarke et al. (1995a), the more intensive use of scrub by the donkeys can be at least partly explained by the scattered distribution of the preferred grassland patches. Yet more research is needed to find out whether the intrinsic differences between donkeys and other horses contribute to absolute differences in habitat use and diet composition. One possibility would be to examine the foraging behaviour of both equid species in areas where they graze together. However, since differences in habitat use and/or diet composition observed in such a situation could very well be the result of interspecific competition, the foraging behaviour should also be investigated for each species when grazing alone in the area. Apart from that, the factor time should also be taken into account, as the flexible habitat use of the donkeys in Houtsaegerduinen over the three consecutive years amply demonstrated. Long-term investigations seem to be required in order to formulate conclusions on the differences in habitat use and foraging behaviour of different equid species (and breeds) in heterogeneous landscapes. It is equally of primordial significance that more (veterinary) research is performed on the possible physiological and other species or breed specific differences. At present, many questions remain unanswered concerning the possible differences in nutritional requirements, digestive efficiency, intake rate, etc. Similarly, it is of utmost importance to have more detailed information on the nutritional characteristics of the study areas, such as productivity and quality of the different plant communities and the nutritive value of different plant species and plant parts.

Land-use related questions are difficult to address experimentally in a thorough manner because of the large spatial and temporal scales involved to capture responses in a meaningful way (Cousins et al., 2003). However, experiments have recently become an important tool in grazing research. They allow the researcher to find clear causal relationships between distinct variables by concentrating on one question and excluding other ‘disturbing’ factors. For instance, our question ‘do donkeys browse more than Shetland ponies?’ could successfully be investigated by well-chosen feeding experiments. Some items will of course be more difficult to analyse experimentally. A question like ‘who forages more in dune scrub?’ implies that the researcher has access to a number of replicas of scrub-grassland configurations. Yet, unlike grassland, scrub cannot be ‘created’ in a short period of time. It would be a scientific challenge to investigate these dune scrub related questions on a more experimental basis, probably along the lines of how Clarke et al. (1995a & 1995b) experimented with heather.
Of course, these questions related to differences in foraging behaviour between different equid species (and breeds) can be extended to other ecosystems. As suggested earlier, donkeys can play a beneficial role in low

productive systems such as heathland, whereas other horse breeds that are more commonly used in grazing management, may be less able to deal with the low forage quantity and quality.
WallisDeVries & Van de Koppel (1998) suggested that the mechanisms determining the distribution of herbivores in spatially heterogeneous environments, urgently need further research. Above we described several mechanisms which we believe to play a role in foraging at the landscape level. These hypothetical paths deserve to be further investigated. Again, experiments may be a useful tool, like the one by Clarke et al. (1995a & 1995b), to investigate how the spatial configuration of different vegetation elements influences foraging behaviour. Future experimental designs may even help to measure the effect of accessibility, social interactions, experienced versus naive animals, breed differences, and so on.

This work aimed to gain insight into the (foraging) behaviour and habitat use of the large herbivores in a low-productive, spatially heterogeneous ecosystem, and to gain insight into the mechanisms of foraging behaviour at the landscape level. We focused on different herbivore species and breeds, since we expected differences in their foraging behaviour and habitat use, due to their morphological and physiological differences. In the end, the results of the study were expected to contribute directly to the understanding of the herbivore impact on the environment. We described the behaviour and habitat use at different hierarchical ecological levels of Highland cattle, Haflinger horses, Shetland ponies and donkeys, free-ranging in several coastal dune reserves. We found significant differences in foraging behaviour and habitat use between the Highland cattle and the Shetland ponies, foraging in the same area, although they showed a high habitat use overlap. Indications are found that foraging behaviour may be dissimilar among equid groups, especially when comparing the donkey (*Equus asinus*) with horse breeds (*Equus caballus*). Possible mechanisms of foraging behaviour have been put forward and we were able to formulate some predictions on herbivore impact. Within the investigated topics many new hypotheses are proposed, hence continuation of this research is desirable.

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Table 6.1

Means on a daily basis of 6 hours, averaged over the 4 seasons and in case of the donkeys averaged over the 3 years (bites from 2 year). Class: Forage class. G: graminoids; F: forbs; W: woody plants. Mean body weight of Highland cows is 481 ± 21 kg, of Highland bulls 520 ± 43 kg. Mean body weight of Shetland mares is 205 ± 8 kg, of donkey mares175 ± 7 kg. Mean body weight of the Haflinger mares is not known.

Dependent variable	**Independent variable**		**Highland cattle**	**Shetland pony**	**Donkey**	**Haflinger horse**
Total grazing time (min)			138	255	202	245
% of Time			38	71	56	68
Total number of bites			4215	8031	2661	-
Bite rate (bites/min.graz.)			29,2	31,5	14,3	-
	Habitat type					
Time (min)	grassy habitat		82	197	140	233
	scrub		33	32	41	7
	woodland		23	25	21	5
% of Grazing time	grassy habitat		59	77	70	95
	scrub		24	13	20	3
	woodland		17	10	10	2
Number of bites	grassy habitat		3171	6485	1965	-
	scrub		567	693	51	-
	woodland		477	853	45	-
% of bites	grassy habitat		75	81	74	-
	scrub		14	9	17	-
	woodland		11	10	9	-
	Class					
Number of bites	graminoids		3650	7281	2123	-
	forbs		354	735	287	-
	woody plants		210	5	251	-
% of bites	graminoids		87	91	80	-
	forbs		8	9	11	-
	woody plants		5	0	9	-
	Habitat type	**Class**				
% of bites	grassy habitat	G	65	74	59	-
		F	6	7	8	-
		W	4	0	7	-
	scrub	G	12	8	14	-
		F	1	1	2	-
		W	1	0	1	-
	woodland	G	10	9	7	-
		F	1	1	1	-
		W	0	0	1	-

Table 6.2

Jacobs' index of selection (1974).

No selection (o): -0.08 < Index < 0.08. Avoidance (-): -0.4 < index < -0.08. Strong avoidance (—): index < -0.4.

Preference (+): 0.08 < index < 0.4. Strong preference (++): index > 0.4.

C: Highland cattle; P: Shetland ponies; D: donkeys; H: Haflinger horses

Habitat type/Vegetation unit	Westhoek			Houtsaegerduinen	
	Area	C	P	Area	D
Grasslands	9 %	++	++	4,7 %	++
Moss dunes & open vegetation	11 %	—	-	7,8 %	++
Rough grasslands	8 %	-	++	4,1 %	++
Grasslands with shrub invasion	7 %	+	+	2 %	+
Rough vegetation	9 %	o	o	3,55 %	++
Scrub	41 %	-	—	67 %	—
Woodland	14 %	+	-	10,85 %	o

	Ghyvelde	
	Area	H
Moss dunes	35 %	-
Carex-dominated grasslands	32 %	++
Rough vegetation	3 %	—
Scrub	7 %	—
Woodland	23 %	—

Table 6.3

Mean grazing time per 6 hrs (min.) and mean daily grazing time per ha (min./ha) for C: Cattle; P: Ponies; D: Donkeys.

Mean body weight of Highland cows is 481 ± 21 kg, of Highland bulls 520 ± 43 kg. Mean body weight of Shetland mares is 205 ± 8 kg, of donkey mares 175 ± 7 kg.

Vegetation	Westhoek-South				Houtsaegerduinen			
	2001				1998		2000	
	C	C	P	P	D	D	D	D
	min.	min./ha	min.	min./ha	min.	min./.ha	min.	min./ha
Grasslands	39,3	7,02	77,8	13,89	37,9	9,93	19,8	5,19
Moss dunes & open veg.	2,3	0,36	14,2	2,15	66,3	10,48	31,9	5,05
Rough grasslands	9,0	1,96	44,0	9,57	30,6	9,43	22,2	6,51
Grasslands + shrub invas.	19,5	4,64	34,4	8,19	7,1	4,35	8,2	5,07
Rough vegetation	11,8	2,15	26,8	4,88	9,6	4,75	48,8	13,07
Scrub	33,3	1,34	32,4	1,31	36,5	0,67	49,8	0,91
Woodland	22,9	2,66	25,0	2,91	43,8	4,50	4,2	0,54

SAMENVATTING

Shetland ponies, Westhoek-South (foto: Indra Lamoot)

Inleiding en doelstelling

Grote herbivoren in een heterogene omgeving

In het natuurlijke landschap zijn voedselbronnen verdeeld over een mozaïek van patches van een variërende grootte en vorm en met een fluctuerende kwantiteit en kwaliteit aan voedsel. Vrijgrazende herbivoren moeten constant foerageerbeslissingen nemen om aan hun noden te voldoen in deze wisselende -zowel in de ruimte als in de tijd- aanwezigheid van voedsel. De relatie tussen het dier en zijn voedselbron, en dus zijn foerageergedrag, wordt zowel bepaald door kenmerken eigen aan het dier als door eigenschappen van zijn omgeving.

In een heterogene omgeving zal het foeragerende dier meer beslissingen moeten nemen dan in een homogene omgeving. Deze beslissingen situeren zich op verschillende hiërarchische niveaus: regionaal niveau, landschapsniveau, niveau van de plantengemeenschap, niveau van de patch (zie Senft et al. 1987). Beslissingen op een hoger niveau beïnvloeden beslissingen op een lager niveau. Elementen die meespelen in de beslissingen op de lagere niveaus zijn vooral gerelateerd aan de beschikbaarheid en kwaliteit van voedsel , zoals energie-, eiwit-, minerale inhoud, verteerbaarheid, afwezigheid van gifstoffen, afwezigheid van morfologische defensiesystemen. In een natuurlijke omgeving variëren deze factoren in de ruimte en in de tijd. Op de hogere niveaus spelen ook elementen niet gerelateerd aan voedsel een rol, bvb. aanwezigheid van beschutting en water.

De voedselbehoeften van grote herbivoren kunnen variëren tussen herbivoortypes, soorten, rassen en zelfs tussen verschillende individuen van eenzelfde ras. Verteringssysteem, metabolische snelheid, lichaamsgrootte zijn enkele van de factoren die deze verschillen in behoeften tussen types, soorten en rassen bepalen en beïnvloeden. Lichaamsgrootte, leeftijd, reproductie, gezondheid zijn elementen die de variatie in behoeften tussen individuen van eenzelfde ras kunnen bepalen.
Runderen en paarden hebben een verschillend verteringsapparaat. Beiden doen beroep op cellulose-verterende micro-organismen voor de vertering

van hun vezelrijk voedsel, maar doen dat elk op een eigen manier. De voor- en nadelen kunnen als volgt worden samengevat. Herkauwers, zoals runderen, bereiken een hogere verteringsefficiëntie van vezelrijk voedsel dan paarden, maar zijn beperkt in hun opname door hun trage verteringsproces. Paarden verteren het voedsel minder efficiënt, maar het voedsel gaat sneller doorheen het verteringssysteem. Ze kunnen daardoor meer voedsel opnemen en compenseren zo de geringere vertering. Een ander voordeel van het systeem van de runderen is dat ze beter in staat zijn om giftstoffen in planten te neutraliseren. Naast het specifieke verteringssysteem verschillen runderen en paarden o.a. in de morfologie van de monddelen en vaak ook in lichaamsgrootte. Al deze ongelijkheden kunnen bijdragen tot een ander foerageergedrag en habitatgebruik van de beide grote grazers.

Hoewel de informatie hierover beperkt is lijken er toch noemenswaardige variaties in o.a. verteringsefficiëntie te bestaan tussen verschillende soorten paardachtigen. Vooral de ezel lijkt specifieke capaciteiten te hebben. Ezels houden hun voedsel langer in hun verteringssysteem dan andere paardachtigen en bereiken een hogere vertering van droge stof, energie, ruw eiwit en vezelfracties. Bovendien zou hun lagere vrijwillige voedselinname per eenheid metabolisch gewicht t.o.v. pony's, wijzen op een lagere metabolische snelheid. Een lagere metabolische snelheid impliceert ook dat de ezel lagere behoeften heeft. Het is niet uitgesloten dat verschillende paardenrassen ook kleine variaties in o.a. metabolische snelheid en verteringscapaciteiten vertonen, maar daarover is nog minder geweten.

Naast de verwachte verschillen in foerageergedrag tussen types en soorten herbivoren, is recent ook de aandacht gevestigd op de mogelijke verschillen in foerageergedrag tussen rassen. Aldus, mag deze factor binnen het begrazingsbeheer in natuurbehoud niet verwaarloosd worden.

Habitatgebruik en natuurbehoud

Grote herbivoren, zoals paarden en runderen, worden in veel natuurgebieden in West-Europa geïntroduceerd in functie van het natuurbeheer. Het aantal gebieden waar begrazingsbeheer wordt toegepast is ook in Vlaanderen de laatste decennia sterk toegenomen. Van de grote grazers wordt verwacht dat ze de biodiversiteit van het natuurgebied in stand houden of vergroten.

Op het einde van de jaren ’90 werd in verschillende natuurreservaten aan de Vlaamse kust met begrazingsbeheer gestart. Op dat moment was er slechts weinig kennis voorhanden over de mogelijkheid dat de grazers in dergelijke nutriënt-gelimiteerde, struweel-gedomineerde terreinen kunnen overleven zonder problemen enerzijds, en anderzijds of de grazers kunnen voldoen aan de beheersdoelstellingen. De beherende instantie introduceerde verschillende soorten grote grazers zodat kon geëvalueerd worden welke soorten (rassen) het best een antwoord boden op zowel de ‘survival-vraag’ als de ‘impact-vraag’. In de verschillende gebieden grazen nu schapen, runderen, paarden en ezels. De specifieke beheersdoelstellingen variëren naargelang het natuurgebied, maar globaal worden volgende doelstellingen geformuleerd voor het begrazingsbeheer in de duinen. Begrazing moet de uitbreiding van dominante, zich snel uitbreidende grassoorten en struweelsoorten verhinderen, moet het open karakter van de specifieke duinvegetaties helpen behouden of herstellen, en moet in de monotone, soortenarme vegetaties voor een verhoogde structurele diversiteit zorgen.

Doelstelling en hypotheses

Dit onderzoek beoogt inzichten te verwerven in het (foerageer-)gedrag en habitatgebruik van grote herbivoren in een laag-productieve omgeving, met een zekere ruimtelijke en temporele heterogeniteit. We focusten op verschillende herbivoorsoorten en -rassen (Schotse hooglandrunderen, Shetland pony’s, Haflinger paarden en ezels), omdat we verschillen in hun foerageergedrag verwachtten als gevolg van de fysiologische en morfologische verscheidenheid. Uiteindelijk kunnen de resultaten ook bijdragen tot het begrijpen van de herbivoorimpact.

De volgende hypotheses werden geformuleerd:

- We verwachten dat runderen en paarden, die in een laag-productieve omgeving leven waar geprefereerde graslanden (met hoog-kwalitatieve grassen) slechts een klein deel van het leefgebied uitmaken, een breder habitatgebruik zullen vertonen om aan hun behoeften te voldoen. De runderen en paarden worden verondersteld ook in (door grote herbivoren) minder gegeerde vegetatietypes, zoals struweel en bos, te foerageren.

- Aangezien de gebieden een seizoenale variatie in voedselbeschikbaarheid en –kwaliteit vertonen, verwachten we dat de dieren hun foerageergedrag hieraan zullen aanpassen, met een verhoogde graasactiviteit in struweel en bos gedurende herfst en winter.
- We veronderstellen dat runderen en paarden zullen verschillen in sommige aspecten van hun foerageergedrag aangezien beide herbivoortypes aanzienlijke fysiologische en morfologische verschillen vertonen. Wanneer beide soorten in eenzelfde gebied grazen wordt nichedifferentiatie verwacht: beide soorten zullen ofwel in ander vegetatietypes grazen, ofwel zullen ze andere niches begrazen met een andere soortensamenstelling of vegetatiehoogte wanneer ze in dezelfde types foerageren.
- Omdat zogende dieren hogere voedselbehoeftes hebben in vergelijking met niet-zogende dieren, verwachten we dat zogende merries een aangepast foerageergedrag zullen vertonen t.o.v. niet-zogende merries. We voorspellen dat zogende merries een hogere opname bereiken door langer te grazen en/of sneller te happen en als dusdanig meer happen te nemen.
- In tegenstelling tot paarden grazend in kleinere weides, verwachten wij dat vrij-foeragerende paarden in heterogene gebieden hun defecatiegedrag niet concentreren in latrinegebieden, maar simpelweg defeceren waar ze grazen.
- Aangezien verschillende paardachtigen variëren in morfologische en fysiologische aspecten, veronderstellen we dat verscheidende paardensoorten en –rassen variaties zullen vertonen in hun foerageergedrag. Graasduur, vegetatieselectie, biomassaconsumptie en consumptie van houtige gewassen kan variëren tussen paardachtigen, vooral wanneer de ezel wordt vergeleken met Haflinger paarden en Shetland pony's.

Studiegebieden

Het veldonderzoek werd uitgevoerd in vier studiegebieden (Figuur 1.1), gesitueerd in drie natuurreservaten: Westhoek, Houtsaegerduinen en Ghyvelde. De eerste twee bevinden zich in de Belgische kustduinen nabij de Franse grens. Ghyvelde is een oud duingebied in Frankrijk vlakbij de noord-

Franse kust en grenzend aan een gelijkaardig duingebied in België. Al deze gebieden zijn relatief nutriëntarme systemen (Tabellen A.1-A.5), met een ruimtelijk heterogeen vegetatiepatroon (Kaarten A.1-4). Grote herbivoren werden in de vier terreinen geïntroduceerd als beheersmiddel, ze zijn er vrij-foeragerend en blijven er jaarrond.

De vier studiegebieden zijn:

- Westhoek-Zuid (ca 60 ha) waar een kudde Shetland pony's en een kleine groep Schotse hooglandrunderen graast
- Westhoek-Noord (ca 54 ha) wordt begraasd door Konikpaarden en Schotse hooglandrunderen
- Houtsaegerduinen (ca 80 ha) met ezels als grazers
- Ghyvelde (ca 75 ha) wordt begraasd door Haflingerpaarden

Foerageergedrag en habitatgebruik van grote herbivoren in kustduinreservaten

Haflinger paarden, Shetland pony's en ezels in de duinen vertonen gelijkaardig time-budget als andere vrij-foeragerende paarden in een gematigd klimaat. Gedurende de dag wordt het grootste deel van hun tijd besteed aan grazen. De Schotse Hooglandrunderen spenderen minder tijd aan grazen dan de paarden.
De gemiddelde graasduur per dag varieert tussen de seizoenen, met de kleinste graasduur in de zomer, zowel bij de paarden als de runderen. Dit is mogelijks een aanpassing aan voedselbeschikbaarheid en –kwaliteit. Alle herbivoren spenderen het grootste deel van hun graasduur in de gras-gedomineerde vegetaties.

Wij verwachtten een duidelijke habitat shift van deze grazige vegetaties naar het struweel of het bos gedurende de seizoenen met lage primaire productie, in het bijzonder in de winter. Hoewel er een verminderde graasactiviteit in de gras-gedomineerde vegetaties in de winter is vastgesteld, werd onze hypothese niet volledig bevestigd. De Haflinger paarden foerageerden niet meer in het struweel of bos gedurende de winter, maar verhoogden verrassend genoeg hun graasduur in de zeer laagproductieve mosduinen gedurende die periode. Shetland pony's en Schotse Hooglandrunderen foerageerden meer in het struweel in de herfst en de winter, maar enkel de runderen verhoogden hun browse activiteit in het struweel, terwijl de pony's er hun dieet van vnl. grassen behielden. Het bos kende een hogere graasdruk in de lente, zowel door de pony's als de runderen, maar niet in de winter of herfst. Het habitatgebruik van de ezels bleek zeer flexibel en veranderde gedurende de drie onderzoeksjaren. In vergelijking met de zomer en de lente werd in de herfst en winter van 1998 meer in het bos gegraasd, terwijl in de herfst en winter van 1999, maar vooral van 2000 duidelijk meer in het struweel werd gefoerageerd. Runderen en ezels vertonen de duidelijkste habitatshift van de grazige vegetaties naar struweel en bos in herfst en winter, en beantwoordden dus het meest aan onze vooropgestelde hypothese.

Dieetsamenstelling (aandeel grassen, kruiden en houtige planten in het dieet) van Shetland pony's, Hooglandrunderen en ezels werd onderzocht. De drie soorten zijn echte “grazers” met vooral grassen (in de brede zin, dus ook zegges en russen) in hun dieet. Desalniettemin is de dieetsamenstelling afhankelijk van het seizoen en de vegetatie waarin gefoerageerd werd. In het geval van de ezels analyseerden we ook in hoeverre Dieetsamenstelling veranderde over een periode van twee jaar, en concludeerden dat, net zoals het habitatgebruik, de dieetsamenstelling flexibel is over de tijd.

Wij veronderstelden dat runderen en pony's meer onderlinge variatie in dieetsamenstelling zouden vertonen. Maar beiden concentreerden zich op grassen. Een belangrijk verschil is echter dat de runderen houtige planten consumeerden, terwijl de pony's dat heel zelden deden. In de zomer en de herfst aten de runderen relatief gezien ook meer kruiden dan de pony's. In de lente verhoogden de pony's hun proportie kruiden in het dieet aanzienlijk ten opzichte van de runderen, terwijl deze laatste in de lente nog meer houtige planten opnamen.

Van de ezels werd verwacht dat zij meer zouden browsen dan andere paardachtigen. Zoals hierboven gesteld, bestaat het dieet van de ezels in de Houtsaegerduinen echter voornamelijk uit grassen. Toch browsten de ezels aanzienlijk meer dan de pony's in Weshtoek-Zuid en vertoonden een browse activiteit vergelijkbaar met die van de runderen.

Een ander element van het habitatgebruik is de manier waarop herbivoren hun faeces verspreiden in hun leefgebied. Paarden, die vrij foerageren in grote, heterogene gebieden, vertonen geen latrinegedrag, zoals paarden gestationeerd in kleinere weides. Haflinger paarden in Ghyvelde, Shetland pony's in Westhoek-Zuid, Konik paarden in Westhoek-Noord en ezels in Houtsaegerduinen defeceren en urineren waar ze grazen. De ruimtelijke spreiding van de eliminatie door paarden is zeer sterk gecorreleerd aan de ruimtelijke spreiding van het graasgedrag. Mogelijks speelt het aantal dieren per oppervlakte-eenheid een rol in de verklaring van dit verschil met paarden in weides. De heterogeniteit en de primaire productiviteit van de omgeving, alsook parasitaire status van de dieren kunnen van belang zijn. Het besluit dat paarden defeceren waar ze grazen heeft belangrijke gevolgen voor het natuurbeheer.

Verschillen in foerageergedrag tussen herbivoortype, soorten en rassen

Foerageergedrag en habitatgebruik van runderen en paarden is reeds enkele malen vergeleken in diverse ecosystemen in de gematigde regio. Deze studie maakt deze vergelijking echter voor de eerste maal in een kustduinsysteem.
Ondanks het feit dat Schotse Hooglandrunderen een veel groter lichaamsgewicht hebben dan de Shetland pony's consumeren ze eenzelfde biomassa per individu. De verschillen in habitatgebruik en dieetsamenstelling zullen dus de verschillen in impact op de vegetatie bepalen. Beide herbivoren consumeren vnl. grassen, maar runderen consumeren meer kruiden en meer houtige gewassen dan pony's (zoals hierboven reeds gemeld). Wat betreft het habitatgebruik concentreren de pony's hun graasactiviteiten meer in de gras-gedomineerde vegetatietypes dan de runderen. De foerageeractiviteiten van de runderen in het struweel bereiken een piek in de herfst (dan grazen ze evenveel in het struweel als in het grazige habitat), deze in het bos bereiken een piek in de lente (dan grazen ze veel meer in

het bos dan in het grazige habitat). Wanneer de runderen in struweel en bos grazen verhogen ze het aandeel kruiden en houtige gewassen in hun dieet. Toch prefereren zowel de runderen als de pony's te grazen in de graslanden (één van de vijf onderscheiden vegetatietypes binnen het grazige habitat). In deze graslanden grazen de pony's meer dan de runderen in de kortste vegetatiehoogtes.

Dichte, gesloten struwelen lijken een grotere barrière te vormen voor de pony's dan voor de runderen. De hoornen met grote spanwijdte van de Schotse Hooglandrunderen lijken hen te helpen bij het doorkruisen van het struweel.

Runderen lijken ook meer exploratief te zijn. Hun terreingebruik (het gebruik van het gehele beschikbare gebied) was 'breder'.

De ezel spendeerde minder tijd aan het grazen dan de Shetland pony's en Haflingerpaarden. Het aantal genomen happen was veel kleiner bij de ezels dan bij de Shetland pony's. Wij veronderstelden dat ezels een lagere metabolische snelheid hebben en dit in combinatie met de betere verteringscapaciteiten zorgt ervoor dat de ezel in een kortere tijdsduur zijn voedselbehoeften kan invullen. Daarnaast opperden we ook dat de ezel een geringere biomassa per eenheid lichaamsgewicht consumeert dan de pony.

De betere verteringscapaciteit kan er ook toe leiden dat de ezel minder voor kwaliteit moet selecteren in vergelijking met andere paardachtigen. We vonden inderdaad dat ezels binnen de grazige vegetaties niet alleen de meest kwalitatieve vegetatietypes prefereerden, maar ook een preferentie vertoonden voor de minder nutritieve types. Bepaalde eerder laagkwalitatieve grassoorten (bvb. *Festuca juncifolia*) maakten inderdaad een aanzienlijk deel uit van het ezeldieet.

De ezels consumeerden ook een groter aandeel houtige gewassen dan de Shetland pony's. Mogelijks kunnen de ezels beter omgaan dan andere paardachtigen met de hoge lignine-inhoud van deze houtige gewassen, misschien door een aangepast kauwgedrag.

Deze vastgestelde verschillen met pony's kunnen echter ook het gevolg zijn van de verschillen in leefgebied. Meer onderzoek is nodig, maar onze data suggereren alvast dat de ezel een geschikte herbivoor kan zijn voor het begrazingsbeheer in droge laag-productieve gebieden.

Voedselbehoeften zijn mede afhankelijk van de reproductieve staat van een dier, en zijn hoger bij zogende dieren. Wij vonden dat zogende merries inderdaad een aangepast foerageergedrag vertoonden om aan deze verhoogde behoeftes te voldoen, in vergelijking met niet-zogende merries. Zowel de zogende pony's als de zogende ezels verhoogden hun hapsnelheid en niet hun graasduur, met een hoger aantal geconsumeerde happen als gevolg. Daarenboven verhoogden ze hun extra graasinspanningen vooral in deze items die het meest begraasd worden door de paardachtigen in het algemeen.

Mechanismen van het foerageergedrag

Aan de hand van onze veldobservaties suggereerden we enkele mechanismen die volgens ons een rol spelen in het foerageergedrag op het landschapsniveau, naast de algemeen aangenomen elementen zoals voedselbeschikbaarheid en -kwaliteit. Enerzijds onderscheidden we elementen die gerelateerd zijn aan de omgeving van het dier. Anderzijds spelen ook dier-gerelateerde factoren een rol.

Beschikbaarheid (en dus ook bereikbaarheid) en ruimtelijk configuratie van geprefereerde vegetatietypes zal het terreingebruik mede bepalen. Waar deze types meer verspreid zijn als kleinere patches over het ganse leefgebied, zoals in Houtsaegerduinen, zullen de dieren meer genoodzaakt zijn om zich te verplaatsen en meer op zoek te gaan naar alternatieve graasplekken. Ook minder gegeerde vegetatietypes zullen meer begraasd worden, omdat de herbivoren er ook meer in contact mee komen vanuit de kleinere grazige patches.

De aanwezigheid van water in het gebied bepaalt mede het terreingebruik. In Westhoek-Zuid bevinden er zich meerdere poelen in de zeer intens begraasde, grote graslandpatches. Wij vermoeden dat met de locatie van de poelen op een grotere afstand van deze gegeerde graasplaatsen, de dieren er iets minder zouden grazen. Wellicht speelt de locatie van water een geringere rol in het geval van de ezels aangezien deze een veel geringere drinkbehoefte vertonen dan pony's.

Verschillen in verplaatsingspatronen tussen soorten en rassen kan een rol spelen in het gebruik van de omgeving. We vermeldden reeds dat runderen veel gemakkelijker zich door een dicht struikgewas verplaatsen dan pony's. Ook de meer recente ervaringen van een herbivoor kunnen bijdragen tot een efficiënter terreingebruik. Graasden de herbivoren vóór introductie in een homogeen of heterogeen terrein? Daarenboven, ervaren individuen die al jaren in een heterogeen, complex gebied grazen, worden beter niet uit een gebied weggehaald aangezien zij hierover een gedegen kennis beschikken. Zij gebruiken hun leefgebied op een efficiëntere manier dan nieuwkomers.

Tenslotte, kuddestructuren beïnvloeden ook het terreingebruik. In Westhoek-Zuid stelden wij vast dat gedurende de bronstperiode de hengst de merries meer bijeen hield dan gedurende de rest van het jaar. Een groepje jonge hengsten foerageerde niet in de nabijheid van de haremgroep. De aanwezigheid van dergelijke groep verbreedt het algemeen terreingebruik.

Impact van de herbivoren op hun omgeving

De duidelijkste impact van de herbivoren op de vegetatie wordt verwacht in de plantengemeenschappen waarin de grootste foerageeractiviteit wordt vastgesteld. Anderzijds speelt ook de graasgevoeligheid van een plantengemeenschap een duidelijke rol.

De resultaten tonen dat pony's, runderen en ezels een significante impact op gras-gedomineerde habitats kunnen hebben. Binnen dit grazige habitat kennen niet alle onderscheiden vegetatietypes echter eenzelfde begrazingsdruk, enerzijds omdat ze niet allen even intens begraasd worden, maar ook omdat ze een verschillende oppervlakte hebben. In Westhoek-Zuid kennen de graslanden de grootste begrazingsdruk per hectare, zowel door de runderen als door de pony's. In Houtsaegerduinen varieerde de begrazingsdruk over de jaren. In 1998 kenden de graslanden, ruige graslanden en open vegetaties en mosduinen de grootste begrazingsdruk per hectare, in 2000 was de grootste begrazingsdruk terug te vinden in de ruige vegetaties (Tabel 6.3). De mosduinen worden geacht eerder kwetsbaar te zijn ten aanzien van betreding. Toch lijkt het erop dat de ezels, die vrij intens de mosduinen begrazen, geen zichtbare aantasting veroorzaken van de fragiele

moslaag. Wanneer ze zich enkel door de mosduinen verplaatsen, gebruiken ze de bestaande paden.
Calamagrostis epigejos wordt beschouwd als een problematische, dominante grassoort. Het blijkt één van de meest begraasde soorten te zijn. De vitaliteit van deze dominante soort wordt onderdrukt door begrazing en dit creëert potenties voor andere soorten. Onderzoek heeft reeds de achteruitgang van *C. epigejos* vastgesteld in de graslanden die door deze soort gedomineerd zijn. Dus begrazing lijkt een goed middel om deze soort te bestrijden.

Hoewel de pony's, runderen en ezels een aanzienlijke tijd (maar een veel geringere tijd dan in het gras-gedomineerde habitat) in deze habitat types foerageren, is hun impact hierop minimaal, omdat het aandeel struweel en bos zeer groot is in de studiegebieden (Tabel 6.3). Toch, de herbivoren verhoogden in herfst en winter hun graasactiviteit in het struweel, waar ezels en runderen bovendien houtige soorten consumeerden. *Ligustrum vulgare* en *Salix repens* werden veelvuldig gegeten door respectievelijk ezels en runderen. De potentie is aanwezig dat runderen en ezels een impact hebben op de struweeluitbreiding door deze soorten. Echter, de vermindering van het oppervlakte struweel zal wellicht niet bereikt worden met begrazing als enig beheersmiddel. Daarenboven worden bepaalde houtige soorten helemaal niet of slechts sporadisch aangevreten. *Hippophae rhamnoides,* die als een problematische soort wordt beschouwd, wordt wel gegeten, doch in geringe mate, door de runderen in de Westhoek, maar wordt niet door de ezels geconsumeerd (tenzij af en toe de bessen). Struweeluitbreiding door *H. rhamnoides* zal dus niet verhinderd worden door de ezels.
Schotse Hooglandrunderen hebben niet alleen een potentiële impact door directe consumptie van houtige soorten in het struweel. Door hun grote omvang en wijde horens maken zij het struweel open en minder vitaal wanneer zij zich er doorheen verplaatsen.

Een ander aspect van het foerageergedrag van grote herbivoren is het terreingebruik, nl. de manier waarop de grazers het gehele voor hen beschikbare terrein gebruiken. Het is kenmerkend voor begrazing in een heterogeen landschap dat bepaalde stukken intensief begraasd worden en dat andere zelden bezocht worden. Er zal dus een gradiënt zijn van 'intensief beheer' tot 'beheer van niets doen'. Soorten verschillen in hun terreingebruik. In de Westhoek is de graasdruk van de runderen meer verdeeld over het ganse terrein, in vergelijking met de graasdruk van de pony's. Die laatsten concentreren zich duidelijk meer in en rond een groter, aaneengesloten, grazig deel.

Nutriëntentransfer is vaak aangebracht als één van de invloeden van begrazing. Een afvoer van nutriënten gebeurt vanuit intensief begraasde plaatsen naar zones waar een concentratie van faeces plaatsvindt. Dit fenomeen, reeds vastgesteld in gebieden begraasd door schapen en runderen, vindt echter niet plaats op grote schaal in terreinen begraasd door paarden. Paarden, vrij-foeragerend in relatief grote, heterogenene gebieden defeceren waar ze grazen.
Het eliminatiepatroon heeft ook een rol in de verspreiding van zaden. Grote herbivoren kunnen zaden verspreiden via hun mest (endozoöchorie) of hun vacht (epizoöchorie). Aangezien dat de meest begraasde habitattypes ook de meest bemeste habitattypes zijn, hebben zaden van plantensoorten geconsumeerd in de gras-gedomineerde vegetatietypes veel kans om geëlimineerd te worden in gras-gedomineerde types

Verder onderzoek

Het is moeilijk om uitspraken te doen over verschillen in graasgedrag en habitatgebruik tussen verschillende soorten (en rassen) herbivoren, wanneer deze soorten in verschillende terreinen grazen. De beschreven verschillen kunnen evenzeer het effect zijn van de verschillen tussen de leefgebieden, als het gevolg zijn van de dier-specifieke kenmerken. Alle studiegebieden zijn kustduingebieden, binnen eenzelfde klimaat, maar toch met veel ruimtelijke verschillen in vegetatiepatronen. Ruimtelijke heterogeniteit wordt bepaald door vele factoren, o.a. door beschikbaarheid van de onderscheiden habitattypes, alsook de ruimtelijke configuratie van die types. Op zijn beurt bepaalt de ruimtelijke heterogeniteit in grote mate het habitatgebruik. Toekomstig onderzoek naar de verschillen in foerageergedrag tussen paardachtigen moet deze variatie tussen studiegebieden uitsluiten. Dat kan door de verschillende herbivoren in eenzelfde gebied te laten foerageren, zoals in het geval van de studie over pony's en runderen. Nochtans, indien dan verschillen worden gevonden kan dit ook het gevolg zijn van competitie. De soorten voor een periode apart in het gebied laten grazen, kan dit effect voorkomen. Daarenboven, willen we er ook op wijzen dat het foerageergedrag een flexibel item is, zoals aangetoond in het ezelonderzoek. Het lijkt er dus op dat langetermijn-onderzoek nodig is.

Recent worden ook experimentele set-ups ontworpen om specifieke begrazings-gerelateerde vragen te beantwoorden. Deze manier van onderzoek heeft het grote voordeel dat op één vraag kan geconcentreerd worden en dat 'storende factoren' worden uitgesloten. Voor heel wat vragen i.v.m. habitatgebruik en foerageergedrag is het nog volledig 'vissen' naar de mogelijke mechanismen die dit gedrag mede bepalen. Experimenten kunnen hier een geschikt middel zijn om de invloed van gesuggereerde mechanismen te achterhalen. Naderhand dienen deze bevindingen in een meer natuurlijke situatie geverifieerd te worden.

Ook het onderzoek naar het habitatgebruik van de grote grazers in de duinen kan op deze manier worden benaderd. Voorbeelden van experimentele designs zijn vooral voorhanden wat betreft het effect van heterogeniteit in graslanden op het foerageergedrag van de herbivoren. Het is een uitdaging om dergelijke vragen naar het struweel-vraagstuk te verplaatsen.

ABSTRACT

Two konik foals, Westhoek-North (foto: Yves Adams)

Forage resources in the natural landscape are distributed in a mosaic of patches of variable size and shape with a fluctuating quantity and quality of food. Free-ranging herbivores have to make many foraging decisions at different resolution levels, resulting in a foraging behaviour that meets the large herbivores' nutrient and energy requirements. Habitat use is an outcome of the foraging behaviour of the herbivores. The relation between the animal and its food supply, and thus its foraging behaviour and habitat use, are determined by the characteristics of the environment on the one hand and the characteristics of the herbivore on the other. It is evident that the foraging animal has to make more foraging decisions in a heterogeneous than in a homogeneous environment. Different animal species, animal breeds as well as individuals may show considerable variation in their nutritional demands, due to intrinsic as well as extrinsic factors. Digestive system, digestive efficiency, metabolic rate, body size, age, reproductive state, health condition, origin are some of the intrinsic factors lying on the basis of differences in nutritional demands.

Different species and breeds of large ungulates have been introduced into several dune reserves along the Belgian coast as a management measure. The nature conservation expectations of this grazing management are high. However, management results and the predictability of them still carry a high level of uncertainty since little is known about the possible impact of the herbivores on such a relatively low-productive, heterogeneous ecosystem. This research does not aim to evaluate the grazing management in the first place, but aims to gain better insights into the (foraging) behaviour and the habitat use of the large herbivores in such a low-productive environment, with a considerable amount of spatial and temporal heterogeneity. We focus on different herbivore species and breeds, since we expect differences in their foraging behaviour and habitat use, due to their morphological and physiological differences. In the end, the results of the study are expected to contribute directly to the understanding of the herbivore impact. The central hypothesis is that foraging behaviour reflects the nutritional ecology of the herbivores and provides a mean to gain insight in the mechanisms determining herbivore impact at the landscape scale.

The (foraging) behaviour and habitat use of Highland cattle, Haflinger horses, Shetland ponies and donkeys, free-ranging in several coastal dune

reserves, is described at different hierarchical ecological levels. Foraging behaviour and habitat use of Highland cattle and Shetland ponies, foraging in the same area, showed significant differences, although they had a high habitat use overlap. Indications are found that foraging behaviour may be dissimilar among equid groups, especially when comparing the donkey (*Equus asinus*) with horse breeds (*Equus caballus*). We found that equids free-ranging in large heterogeneous areas do not perform latrine behaviour, but defecate where they graze; this is in contrast with horses grazing in pastures. Possible mechanisms of foraging behaviour have been put forward and we were able to formulate some predictions on herbivore impact. Within the investigated topics many new hypotheses are proposed, hence continuation of this research is desirable.

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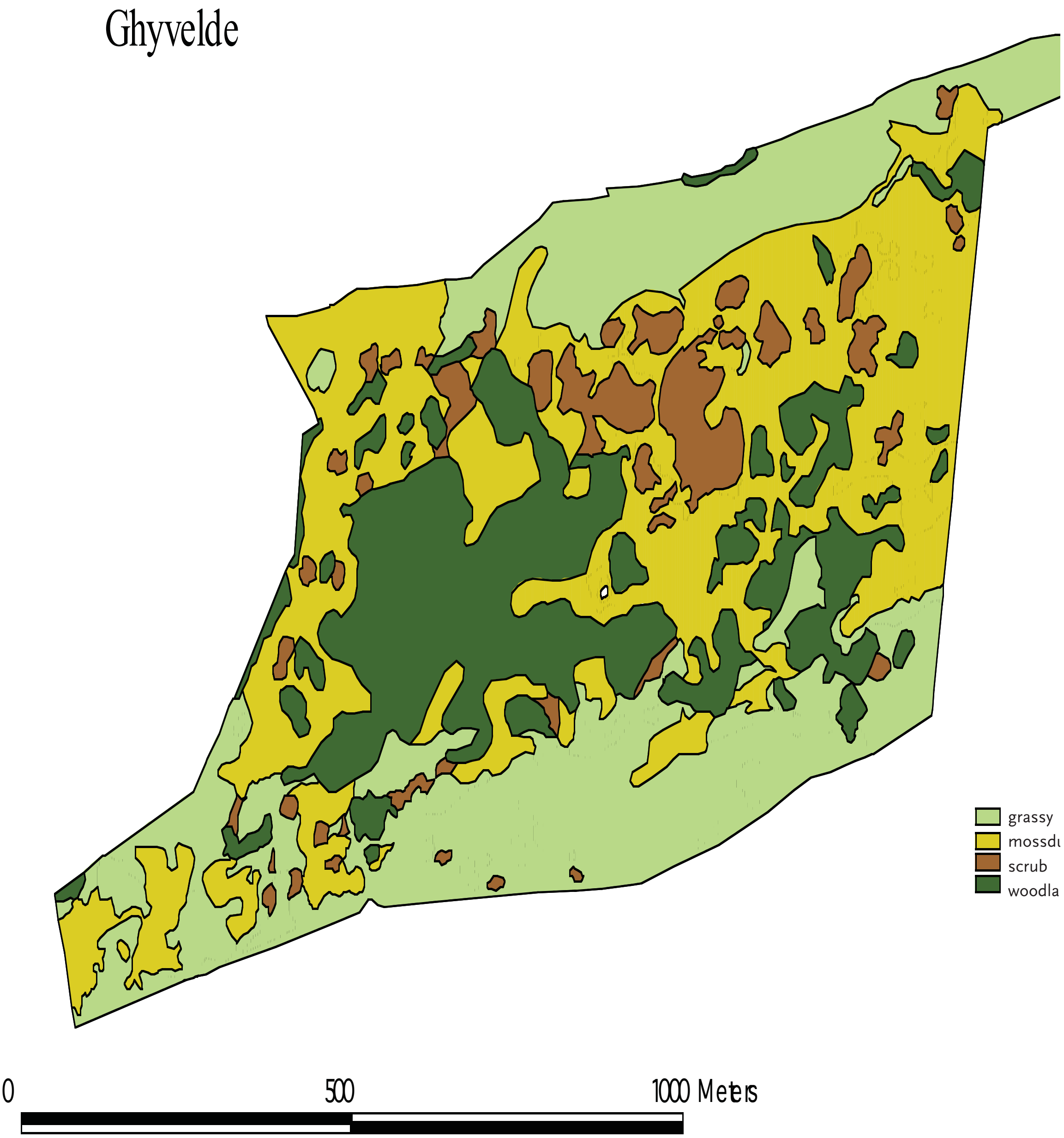
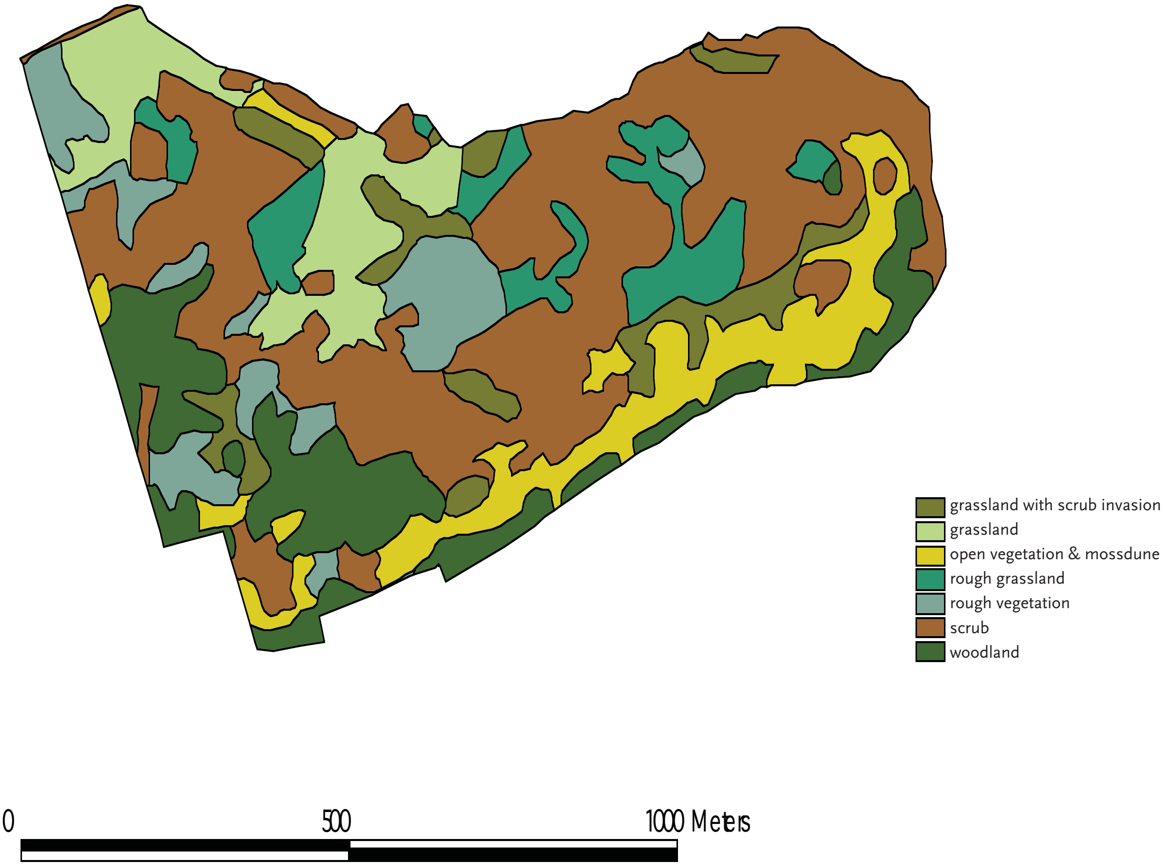
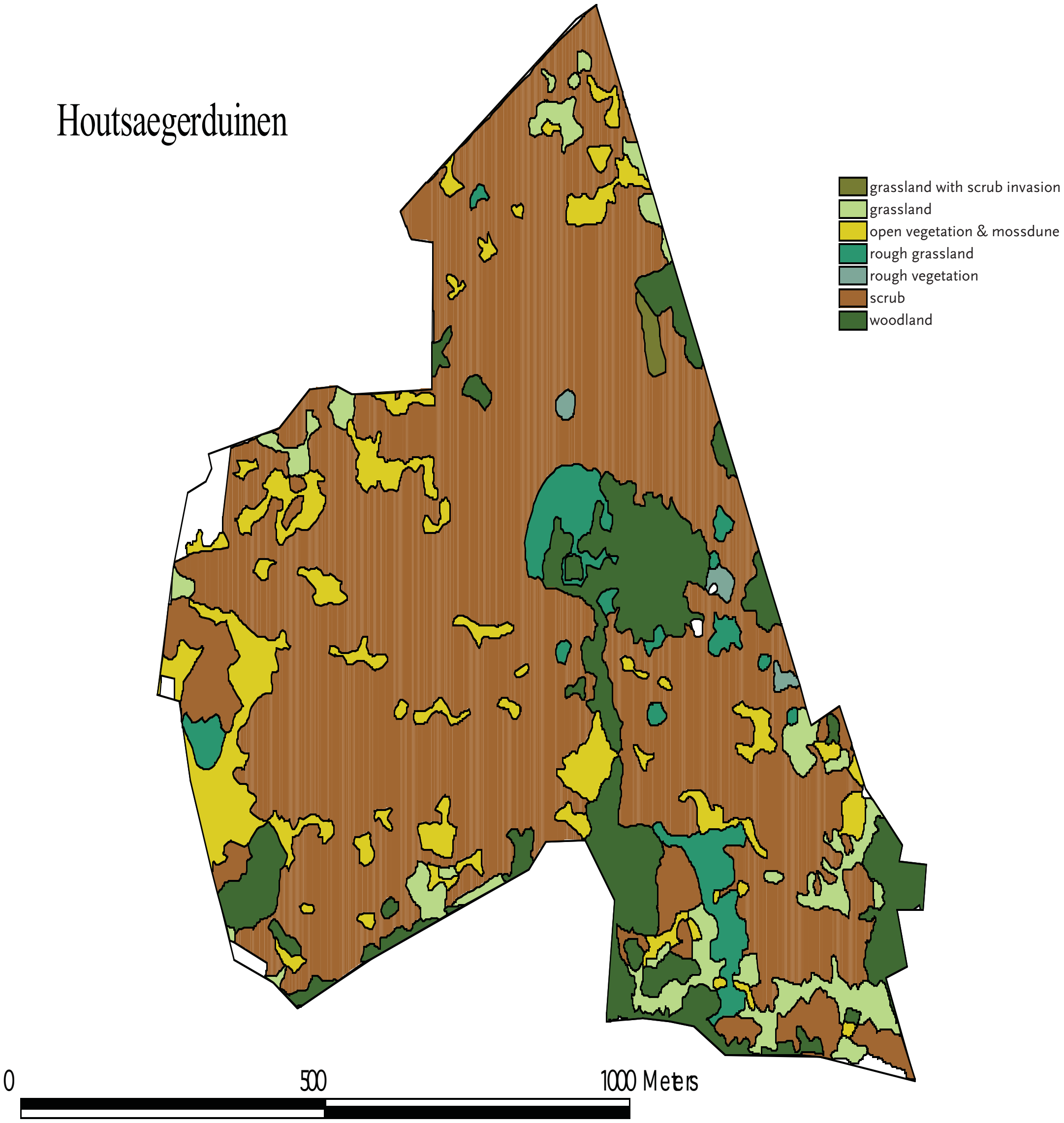
APPENDIX

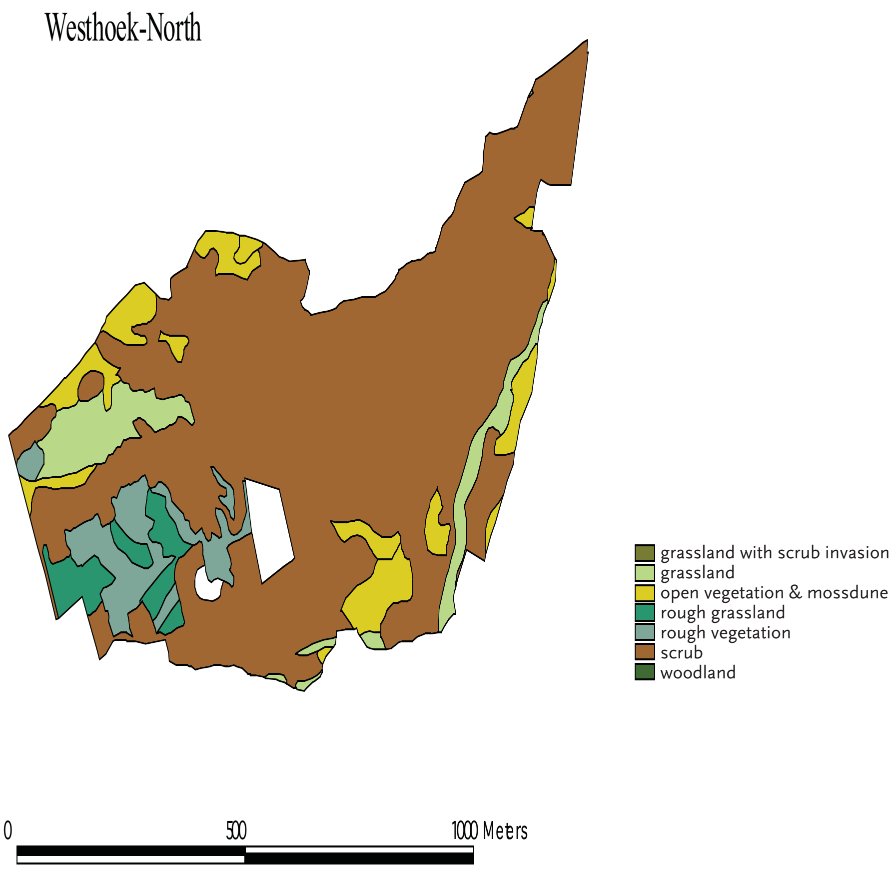
(FOTO: YVES ADAMS)


Ghyvelde
grassy
mossd
scrub
woodla
0
500
1000 Meters

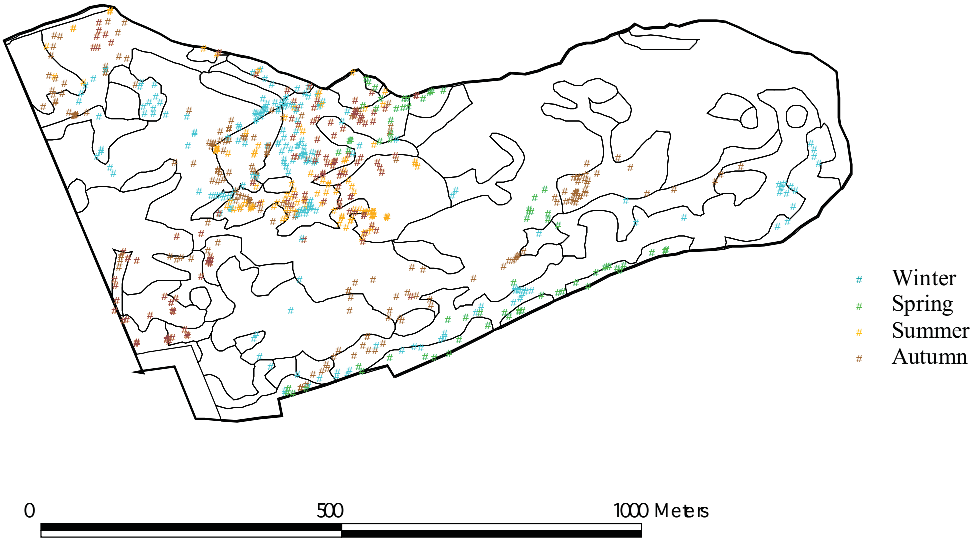
Westhoek-South



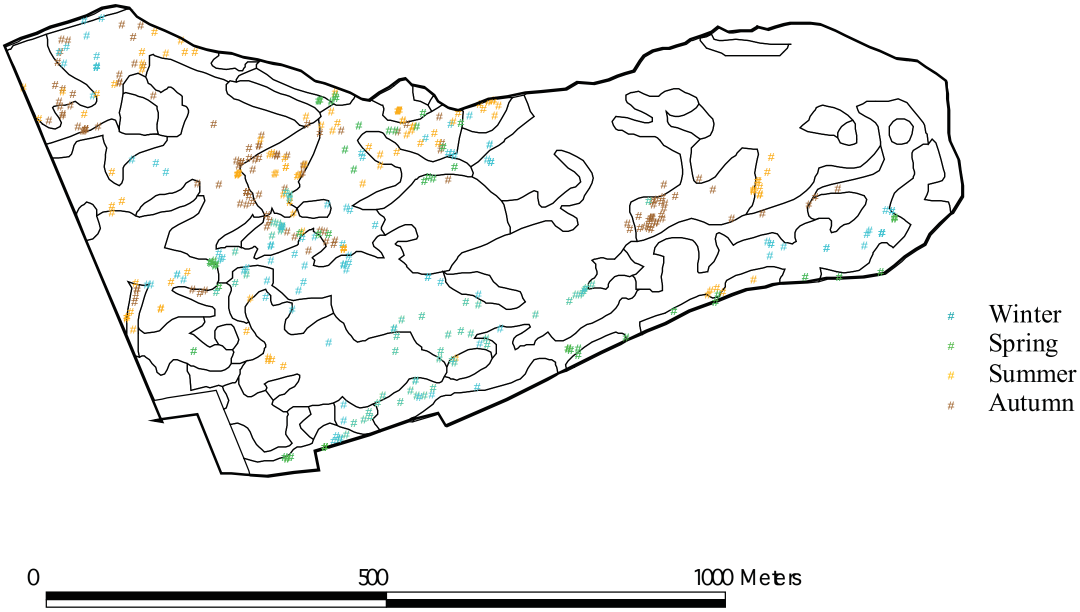

Houtsaegerduinen
grassland with scrub invasion
grassland
open vegetation & mossdune
rough grassland
rough vegetation
scrub
woodland
0
500
1000 Meters

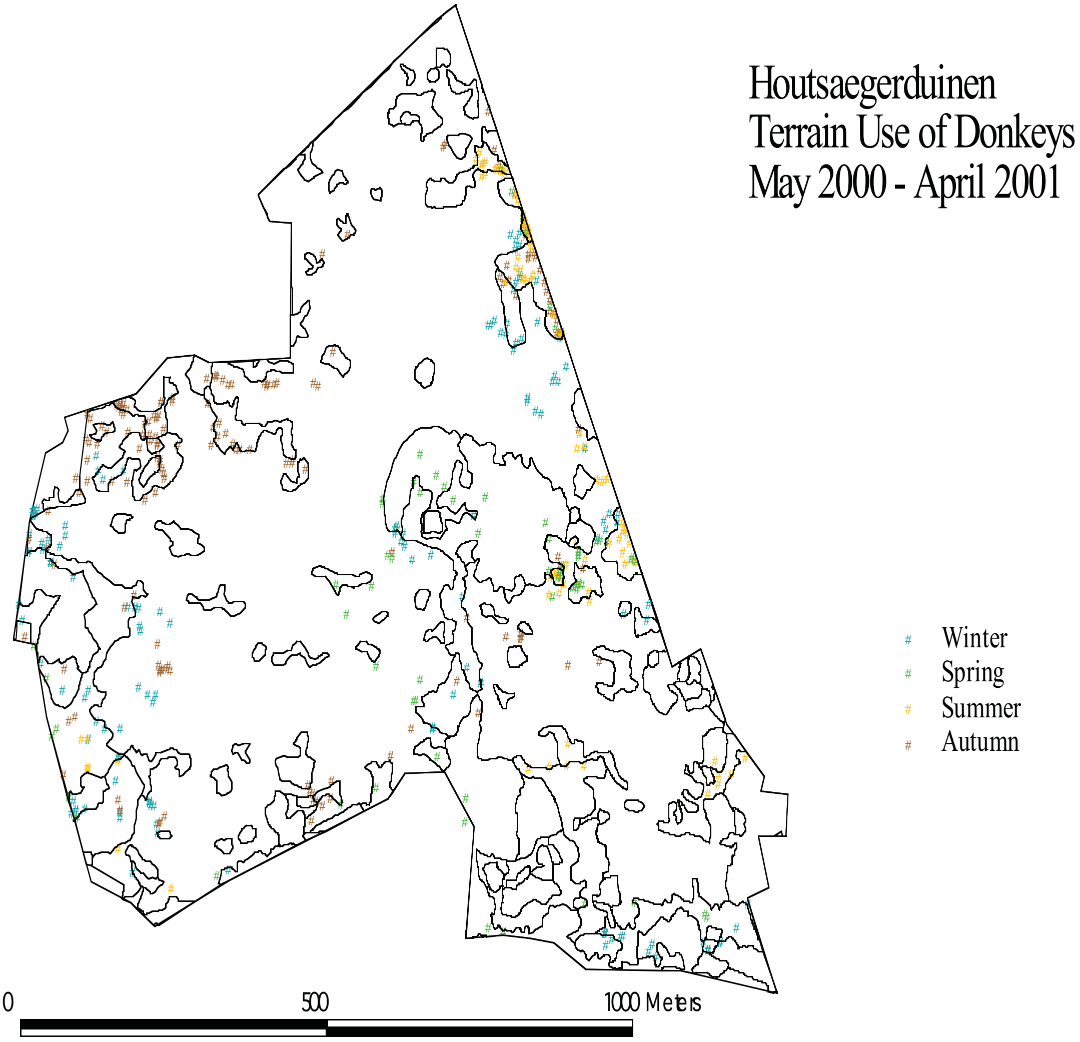

Westhoek-North
grassland with scrub invasion
grassland
open vegetation & mossdune
rough grassland
rough vegetation
scrub
woodland
0
500
1000 Meters

Westhoek - South
Terrain Use of Shetland ponies
Aug 2001 - March 2002



Westhoek - South
Terrain Use of Highland cattle
Aug 2001 - March 2002





Houtsaegerduinen
Terrain Use of Donkeys
May 2000 - April 2001

Table A.1 (unpublished data of Cosyns)

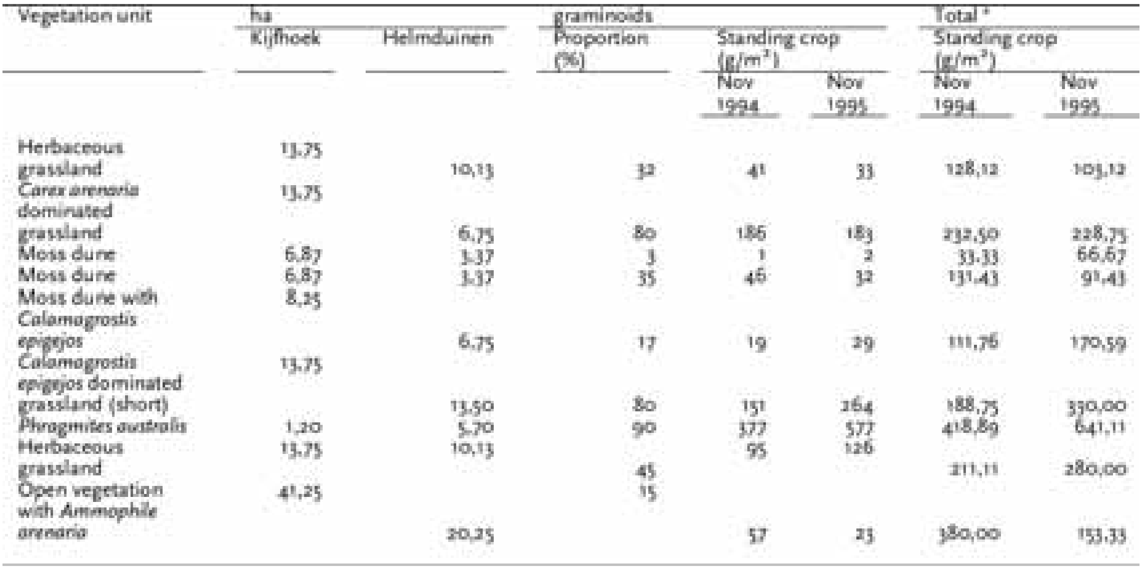
Standing crop of several vegetation units in two grazed dune areas. Vegetation was cut on N plots of 50x50cm, dried, separated in graminoids, forbs and woody plants and weighted. %live: proportion of the standing crop which was live (green) material. Undet.: plant material which could not be identified as graminoid, forbs or woody. Winter: data from February 1999; Summer: data from July 1999.

Area	Season	Vegetation unit	ha	Graminoids		Forbs		Wood		Undet.	N
				g/m^2	%live	g/m^2	%live	g/m^2	%live	g/m_	
Westhoek-South	Winter	Open A1		442,00	24	0,00		0,00			2
		Open A3/A4		25,64	14	0,00		0,00			1
		Moss dune		6,49	100	3,85	75	0,00			4
		Grassland	5.4	59,79	6	9,14	58	0,12	100	26,28	3
		Rough grassland	4.5	387,21	0	20,31	3	0,80	100		4
		Rough vegetation	5.3	227,80	0	5,14	41	83,17	100		6
		Woodland	8.3	1,82	100	26,14	91	2,72	100		5
	Summer	Open A1		485,61	87	2,55	62	0,00			3
		Open A3/A4		14.47	99	2,96	100	0,00			3
		Moss dune		17.77	91	6,17	96	0,00			3
		Grassland	5.4	107,76	77	50,83	100	3,63	100	8,22	7
		Rough grassland	4.5	366,57	61	189,73	100	1,64	100	10,83	10
		Rough vegetation	5.3	155,68	41	152,64	100	206,90	100	2,58	10
		Woodland	8.3	70,14	100	87,96	86	34,88	100	1,46	5
Houtsaegerduinen	Winter	Open A1		146,44	53,62	0		0			1
		Open A3/A4		6,88	100	0,04	100	0			1
		Moss dune		9,07	42,03	2,53		0			6
		Grassland	3,8	73,92	72,67	10	12,8	34,4	100		2
		Rough grassland	3,2	358,51	0,91	0		6,08	100	5,68	5
		Rough vegetation	2,0	186,00	18,82	0,65	20	160	100		4
	Summer	Open A1		1047,12	51,22	0,15	90,90909	0			3
		Open A3/A4		14,06	62,16	0,32	37,5	0			2
		Moss dune		27,62	86,50	13,37	94,31563	0			4
		Grassland	3,8	449,07	100	77,49	96,61906	24,16	100	12,33	7
		Rough grassland	3,2	314,08	82,73	7,86	76,28735	19,95	100		7
		Rough vegetation	2,0	110,47	100	31,17	89,02039	188,93	100	9,33	3

Table A.2 (Meydam, 1996)

Standing crop of exclosures in several vegetation units in Meijendel, a dune area in the Netherlands. Two parts (Kijfhoek/Bierlap, ca 275 ha and Helmduinen, ca 135 ha) are grazed by Galloway cattle and Fjord horses, Proportion of edible graminoids were estimated (unpubl. data Van der Hagen), Estimated values were used to calculate the standing crop of the edible graminoids,

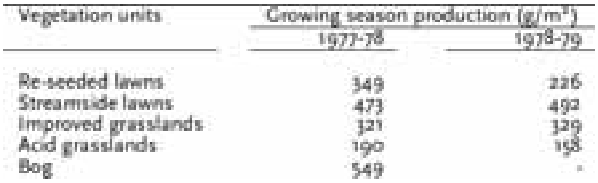
a: we used the data to calculate the total standing crop of the vegetation units.



Vegetation unit	ha		graminoids			Total ᵃ	
	Kijfhoek	Helmduinen	Proportion (%)	Standing crop (g/m²)		Standing crop (g/m²)	
				Nov 1994	Nov 1995	Nov 1994	Nov 1995
Herbaceous grassland	13,75	10,13	32	41	33	128,12	103,12
Carex arenaria dominated grassland	13,75	6,75	80	186	183	232,50	228,75
Moss dune	6,87	3.37	3	1	2	33.33	66,67
Moss dune	6,87	3.37	35	46	32	131.43	91.43
Moss dune with *Calamagrostis epigejos*	8,25	6,75	17	19	29	111,76	170,59
Calamagrostis epigejos dominated grassland (short)	13,75	13,50	80	151	264	188,75	330,00
Phragmites australis	1,20	5,70	90	377	577	418,89	641,11
Herbaceous grassland	13,75	10,13	45	95	126	211,11	280,00
Open vegetation with *Ammophila arenaria*	41,25	20,25	15	57	23	380,00	153,33

Table A.3 (Putman, 1986)

Total annual production of several grazed vegetation units in the New Forest, Great Britain.



Vegetation units	Growing season production (g/m²)	
	1977-78	1978-79
Re-seeded lawns	349	226
Streamside lawns	473	492
Improved grasslands	321	329
Acid grasslands	190	158
Bog	549	-

Table A.4 (Ternier et al. 2001)

Total annual production and crude protein values of several grassland types in the province West-Vlaanderen, Belgium. Crude protein (CP) values expressed as proportion of dry matter.

Grassland type	Main species	Fertilizers	Mowing regime	Total production (g/m^2)	CP (%)	
					1e mowing	regrowth
Grassland managed for botanical diversity	*Elymus repens* *Lolium perenne* *Poa trivialis* *Agrostis* spec. *Bromus hordeaceus* *Alopecurus pratensis* *Holcus lanatus* *Lolium multiflorum* *Senecio jacobaea* *Trifolium repens* *Poa annua* *Arrhenatherum elatius* *Ranunculus* spec. *Cardamine hirsuta*	No	July, (Aug), Okt	950	6,1	13,7
Grassland managed for avifauna	*Elymus repens* *Lolium perenne* *Poa trivialis* *Agrostis* spec. *Bromus hordeaceus* *Alopecurus pratensis* *Holcus lanatus* *Lolium multiflorum* *Senecio jacobaea* *Trifolium repens*	Intermediate level	June, Aug, Okt	1117	6,4	14,6
Classic production grassland	*Elymus repens* *Lolium perenne* *Poa trivialis* *Agrostis* spec. *Bromus hordeaceus* *Alopecurus pratensis* *Holcus lanatus* *Lolium multiflorum*	High level	May, June, Aug, Okt	1410	13,7	14,0

Table A.5 : Nutritive value of several plant species.

Sources : A : unpublished data of Cosyns, E. Results of chemical analyses of hand-plucked samples representing bites. (HS: Houtsaegerduinen; WS: Westhoek-South; WN: Westhoek-North)

B: literature. 1. http://eesc.orst.edu/agcomwebfile/edmat/html/pnw/pnw503/composition.html

2. NRC, 1989

3. Vulink, 2001. Data of the three forage classes in a reed dominated vegetation (OP: Oostvaardersplassen, NL)

4. Isterdael et al. 1990. Three main forage species for sheep grazing in heather (KH: Kalmthoutse heide, B)

All values expresses on a dry matter basis. CP = Crude protein; NDF = Neutral detergent fibre; ADF = Acid detergent fibre; ADL = lignine; SS = Soluble sugars; DE = Digestible energy

Source	Vegetation unit	Species	Area	Season	CP	NDF	ADF	ADL	SS
					(%)	(%)	(%)	(%)	(%)
A	Open A1	*Ammophila arenaria*	HS	Spring	7,1	75,8	43,4	8,8	1,5
				Winter	3,7	74,9	43,6	9,0	2,3
			WS	Summer	3,6	76,2	42,4	9,7	4,9
	Open A3/A4 Moss dune	*Carex arenaria*	HS	Spring	12,9	57,4	27,2	5,3	7,1
				Summer	7,4	66,4	33,1	6,5	6,0
				Autumn	7,2	65,0	32,6	7,3	6,7
			WS	Spring	10,3	59,8	28,6	6,2	8,0
				Summer	9,0	66,7	33,1	7,0	5,2
				Autumn	11,0	69,7	34,5	6,7	2,3
				Winter	7,2	70,7	36,9	7,8	4,1
		Festuca juncifolia	HS	Winter	5,4	71,0	38,1	4,5	3,6
			WS	Spring	8,3	63,5	32,0	4,9	8,6
				summer	5,9	70,1	37,4	5,2	
	Grassland	mix: *Holcus lanatus* *Carex* spec *Juncus* spec *Poa trivialis* *Senecio jacobaea*	WS	Summer	14,7	44,6	21,0	4,8	10,6
				autumn	13,6	50,7	24,9	7,2	5,9
		mix: *Holcus lanatus*	WS	Summer	12,9	56,7	26,8	4,0	6,1
		Calamagrostis epigejos		Autumn	18,3	48,3	21,7	5,1	6,2
		mix: *Holcus lanatus* *Poa trivialis* *Juncus* spec	WS	Summer	12,6	47,4	23,3	5,1	10,9

Source	Vegetation unit	Species	Area	Season	CP (%)	NDF (%)	ADF (%)	ADL (%)	SS (%)	DE (Mcal/kg)
		Agrostis stolonifera	WS	Summer	10,7	61,1	31,2	4,3	6,9	
		Arrhenatherum elatius	HS	Spring	14,1	54,6	26,8	2,9	4,2	
				Summer	4,9	61,3	35,0	4,4	14,6	
				Autumn	18,4	52,5	27,1	5,5	5,5	
				winter	19,4	46,6	21,5	2,3	9,1	
		Galium aparine	HS	Spring	10,7	37,5	24,2	4,7	12,1	
				Summer	10,4	52,1	36,6	8,7	3,3	
			WS	Spring	18,3	32,3	22,9	5,9	2,8	
				Summer	9,1	52,6	35,8	7,7	3,6	
	Rough grassland	*Calamagrostis epigejos*	HS	Spring	15,8	66,5	35,0	5,5	2,4	
				Summer	8,3	76,4	41,4	6,6	1,6	
				Autumn	10,4	73,7	46,4	6,2	2,9	
				winter	7,8	78,2	43,5	7,3	2,2	
		Juncus subnodulosus	WS	Spring	17,0	63,4	27,3	1,5	3,5	
				summer	7,2	73,6	36,5	3,1	1,6	
		mix: *Juncus spec* *Poa spec*	WS	Spring	15,2	54,2	25,8	4,2	7,3	
				Autumn	12,7	51,4	23,2	5,0	12,7	
	Rough vegetation	*Cirsium arvense*	WS	Spring	10,1	47,8	32,8	9,2	0,7	
				Autumn	26,9	36,0	22,9	6,2	3,9	
		Eupatorium cannabinum	HS	Autumn	8,3	43,9	29,3	9,1	2,1	
		Rubus caesius	HS	Summer	11,6	42,6	26,0	7,3	6,6	
				Autumn	9,4	36,7	22,4	5,7	8,3	

Table A.6

Composition of the herds of equids and the group of cattle in the three Belgian nature reserves. The data cover the different study periods used in this work. The situation at the beginning of the year is given.

Study site	Species	year	females				males				Total
			adult	2-year	1-year	newborn	adult	2-year	1-year	newborn	
Houtsaegerduinen 80 ha	Donkeys	jan/98	5				1				6
		jan/99	5			1	1			1	6 + 2
		jan/00	5		2	2	1		1	1	9 + 3
		jan/01	5	2	2		1	1	1	3	12 + 3
		jan/02	7	2		4	4	1	3	3	17 + 7
Westhoek-South 54 ha	Shetland ponies	jan/98	7				1				8
		jan/99	7			2	1			5	8 + 7
		jan/00	8		2	4	-		3	2	13 + 6
		jan/01	8	2	2		1	3	1	2	17 + 2
		jan/02	7	-		3	3	1	2	4	12 + 7
	Highland cattle	jan/98									
		jan/99	1				1				2
		jan/00	1				1			1	2 + 1
		jan/01	1				1	1	1		4
		jan/02	1				2	1			4
Westhoek-North 60 ha	Konik	jan/99	2				2				4
		jan/00	2			1	2				4 + 1
	Highland cattle	jan/99	4								4
		jan/00	4								4

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Different species and breeds of large ungulates have been introduced into several dune reserves along the Belgian coast as a management measure. This research aimed to gain better insights into the (foraging) behaviour and the habitat use of the large herbivores in such a low-productive environment, with a considerable amount of spatial and temporal heterogeneity. We focused on different herbivore species and breeds, since we expected differences in their foraging behaviour and habitat use, due to their morphological and physiological differences. The central hypothesis is that foraging behaviour reflects the nutritional ecology of the herbivores and provides a mean to gain insight in the mechanisms determining herbivore impact at the landscape scale.

The (foraging) behaviour and habitat use of Highland cattle, Haflinger horses, Shetland ponies and donkeys, free-ranging in several coastal dune reserves, is described at different hierarchical ecological levels. Possible mechanisms of foraging behaviour have been put forward and we were able to formulate some predictions on herbivore impact.

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