

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

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## 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 maximum 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 3 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. We discuss the possible role of the donkeys in nature management.

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*Keywords:* Grazing behaviour; Habitat use; Donkey; Equid; Diet composition

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## 1. Introduction

Until the beginning of the 20th century, practically all coastal dunes in Belgium were grazed for agricultural purposes. After several decades of non-grazing, a number of dune areas are being grazed again, but now for reasons of nature management (Provoost et al., 2002). In the late 1990s, 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 limited 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 3 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.

## 2. Materials and methods

### 2.1. 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

2-year-old mares, two adult stallions, one 2-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 (unpublished 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 60.7 mm, 74.8 mm, 56.5 mm and 48.5 mm, respectively (means for the period 1963–2002; Meteo WVL vzw).

Approximately, two-third 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 approximately 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 *H. rhamnoides*, *L. 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  $175 \pm 7$  kg (weighted in May 2000, March and October 2001). The animals are free ranging and remain in the area year round. They receive no additional food.

## 2.2. Behavioural observations

The grazing behaviour and habitat use of the donkeys was investigated discontinuously during a period of 3 years. Four observation periods can be distinguished (Table 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 6-h period, we continuously monitored the behaviour of one focal animal, except for period ‘2001’. Then, two focal animals were observed, each for 3 h. 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: ‘grassland’, ‘rough grassland’, ‘grassland with scrub invasion’, ‘rough vegetation’ and

Table 1  
 Characteristics of the four observation periods

Observation period	Code	Number of session/month	<i>N</i>	Sampling session (h)	Diurnal coverage	Observations
August 1998–May 1999	1998	5–6	43	6	Day + night (0–24 h)	Behaviour, habitat use
August 1999–May 2000	1999	5–6	47	6	Day + night (6–24 h)	Behaviour, habitat use, diet
May 2000–April 2001	2000	3	33	6	Day	Behaviour, habitat use, location
August 2000–July 2001	2001	3	37	2 × 3	Day	Behaviour, habitat use, diet

In the text, we refer to the codes, instead of the observation periods.

‘moss dune and open vegetation’ as described above. During the 2000 period, every 15 min 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).

### 2.3. Data analysis

#### 2.3.1. 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 h) were conducted between 0:00 h and 24:00 h, 58% of which were performed during daytime hours. In 1999, the observations (282 h) took place between 6:00 h and 24:00 h, 75% of which were done during daytime. In 2000, all observations (198 h) 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 6 h 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 (maximum 5 min) of non-grazing activity, e.g., scanning of the environment. When the focal animal stops grazing for more than 5 min, 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 min during a 6 h 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 6 h and total grazing time per 6 h was calculated (Spearman correlation,  $N = 32$ ).

### 2.3.2. *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 (Jacobs, 1974) to describe the habitat preference, while taking into account the availability of the different habitat types. Jacobs' index of selection (1974):  $D_i = (p_i - A_i) / ((p_i + A_i) - (2 \times p_i \times A_i))$  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.

### 2.3.3. *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 arcsinus transformed, other data were logarithmically transformed. Analyses of variance were performed using SAS System V8. Number of d.f. was estimated by the Satterthwaite-method. The positional field data were digitized and processed with ArcView GIS 3.2a.

### 3. Results

#### 3.1. 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/h during the night and 37 min/h during the day. In addition, there was a Year-effect ( $F_{1,167} = 6.68$ ;  $p = 0.011$ ) and a significant interaction DayNight  $\times$  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.

#### 3.2. Time budget during daytime

The time budget of the donkeys in the different seasons, averaged over the 3 years, is presented in Table 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, illustrating the temporal variation in grazing time. 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

Table 2  
Time budget of the donkeys, averaged over the 3 years

	Year		Summer		Autumn		Winter		Spring	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
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
Laying 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

Mean and S.E. as percentages of a 6-h period.

reverse pattern was found for resting time (14.3%, 23.2% and 28.1% in 1998, 1999 and 2000, respectively). In all 3 years (no significant interaction Season  $\times$  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 (Table 2).

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

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

### 3.3. General habitat use

ANOVA analysis clearly shows the habitat use variation among seasons and among years (Fig. 1), since significant interactions Habitat  $\times$  Season ( $F_{6,180} = 2.69$ ;  $p = 0.016$ ) and Habitat  $\times$  Year ( $F_{4,180} = 10.28$ ;  $p < 0.001$ ) occur. The significant three-way interaction ( $F_{12,180} = 1.94$ ;  $p = 0.032$ ) shows that the seasonal variation in habitat use was not similar over the 3 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 3 years. The use of scrub and woodland was variable among seasons and 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 min/6 h, 26 min/6 h and 7 min/6 h in the winter of 1998, 1999 and 2000, respectively). Instead, the use of scrub increased from 1998 to 2000 (27 min/6 h, 57 min/6 h and 95 min/6 h in the winter of 1998, 1999 and 2000, respectively).

From the Jacobs' index of 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 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).

### 3.4. 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  $\times$  Season ( $F_{12,210} = 1.86$ ;  $p = 0.041$ ), Vegetation  $\times$  Year ( $F_{4,210} = 7.58$ ;  $p < 0.001$ ) and Vegetation  $\times$  Season  $\times$  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 three-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

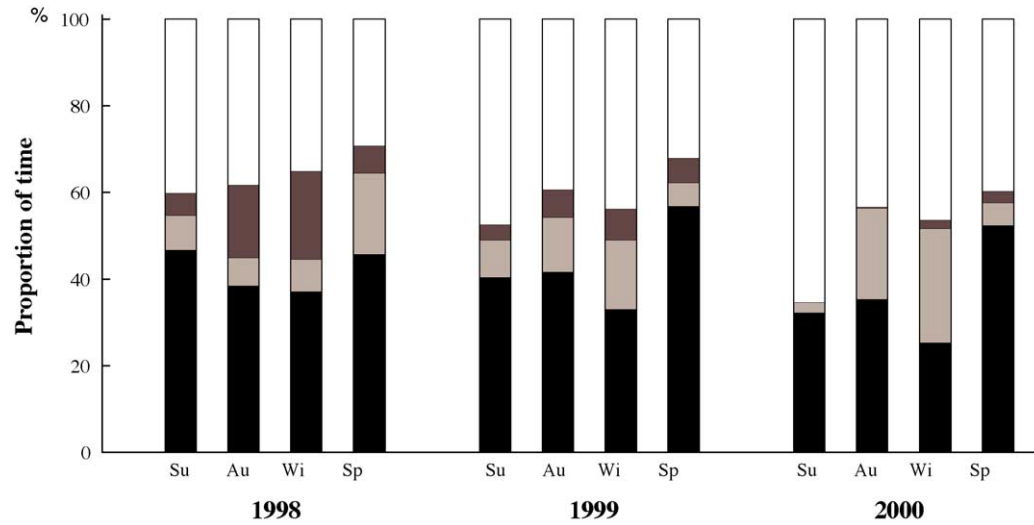


Fig. 1. Habitat use of the donkeys, with its seasonal variation, in the three consecutive years. Black represents the proportion of time spent grazing in the grassy habitat. Light grey: proportion of time spent grazing in scrub. Dark grey: proportion of time spent grazing in woodland. White: proportion of time spent to non-grazing activities. Su: summer, Au: autumn, Wi: winter, Sp: spring.



Table 3  
Jacobs' index of selection

Habitat type	Area (%)	1998	1999	2000
Grassy vegetations	23.3	++	++	++
Scrub	67.0	--	--	--
Woodland	9.7	+	0	--

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

grasslands, in 1998 than in 2000. On the other hand, the donkeys spent more grazing time in rough vegetation in 2000 (Fig. 2).

### 3.5. 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 ( $2006 \pm 394$  bites/6 h,  $2604 \pm 364$  bites/6 h,  $2874 \pm 590$  bites/6 h and  $5273 \pm 701$  bites/6 h 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 ( $10.5 \pm 0.4$  bites/min,  $11.6 \pm 0.9$  bites/min,  $13.6 \pm 1.8$  bites/min and  $21.5 \pm 1.6$  bites/min grazing in summer, autumn, winter and spring, respectively). The factor Season had indeed a significant effect on the variable bite rate ( $F_{3,17.8} = 5.03$ ;  $p = 0.011$ ).

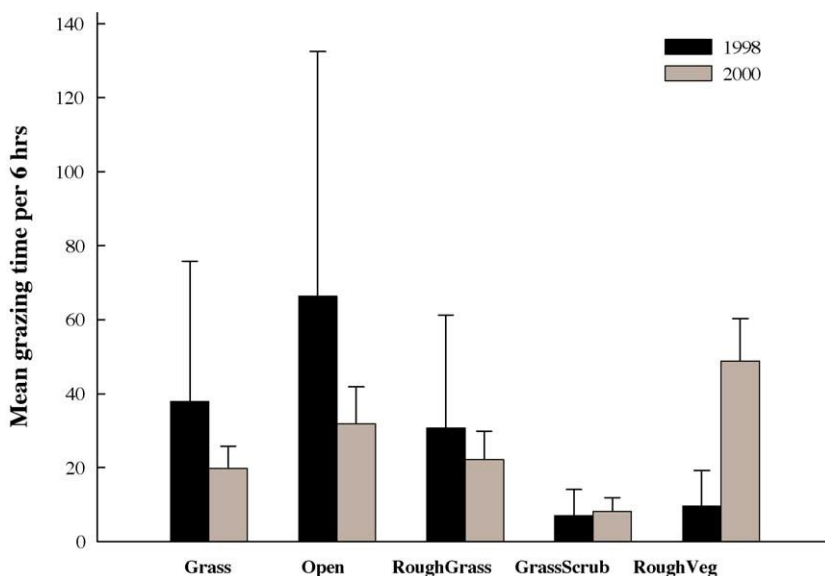


Fig. 2. The use of the grassy habitat in 1998 and 2000. Mean grazing time  $\pm$  S.E. per 6 h (min) in the five vegetation units distinguished within the grassy habitat. Grass: grassland; Open: open vegetation and moss dunes; RoughGrass: rough grassland; GrassScrub: grassland with scrub invasion; RoughVeg: rough vegetation.

Table 4

Plant species from which more than 500 bites were taken during 132 h in 1999 and during 219 h in 2001

1999			2001		
Plant species	Class	% Bites	Plant species	Class	% Bites
<i>C. epigejos</i>	G	31.62	<i>C. epigejos</i>	G	19.15
Mix of graminoids	G	16.43	<i>F. juncifolia</i>	G	14.83
<i>A. elatius</i>	G	12.28	mix of graminoids	G	21.35
<i>F. juncifolia</i>	G	8.13	<i>A. elatius</i>	G	10.36
<i>C. arenaria</i>	G	7.50	<i>C. arenaria</i>	G	5.54
<i>R. pimpinellifolia</i>	W	3.18	<i>L. vulgare</i>	W	3.69
<i>Claytonia perfoliata</i>	F	2.98	<i>Rubus caesius</i>	F	3.30
<i>Elymus repens</i>	G	2.04	<i>U. dioica</i>	F	3.28
<i>Rubus caesius</i>	F	1.78	<i>H. lanatus</i>	G	2.14
<i>L. vulgare</i>	W	1.72	<i>C. vitalba</i>	W	1.64
<i>U. dioica</i>	F	1.61	<i>Galium aparine</i>	F	1.62
<i>A. arenaria</i>	G	1.39	<i>Hieracium umbellatum</i>	F	1.32
<i>Poa trivialis</i>	G	1.20	<i>Poa spec.</i>	G	0.86
<i>Rosa canina</i>	W	0.80	<i>P. alba</i> (+ <i>P. x canescens</i> )	W	0.85
<i>Festuca rubra</i>	G	0.73	<i>A. pubescens</i>	G	0.72
			<i>R. pimpinellifolia</i>	W	0.72
			<i>A. arenaria</i>	G	0.70

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.

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 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% of forbs and 10% of woody plants. However, the diet composition was variable among seasons (Fig. 3). The proportion of bites taken per forage class was significantly affected by the interactions Class  $\times$  Season  $\times$  Year ( $F_{6,257} = 7.60$ ;  $p < 0.001$ ) and Class  $\times$  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 *R. pimpinellifolia* fruits (classified as woody plant) in summer. The donkeys took even more bites of *R. pimpinellifolia* than of *C. epigejos* in summer 1999, while in the other seasons, in the absence of rose hips, *R. pimpinellifolia* was bitten only rarely. In 2001, *R. pimpinellifolia* hips were far less frequently consumed (see Table 4).

Diet composition depended on the foraged habitat type and this varied as well among seasons and between years (Table 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

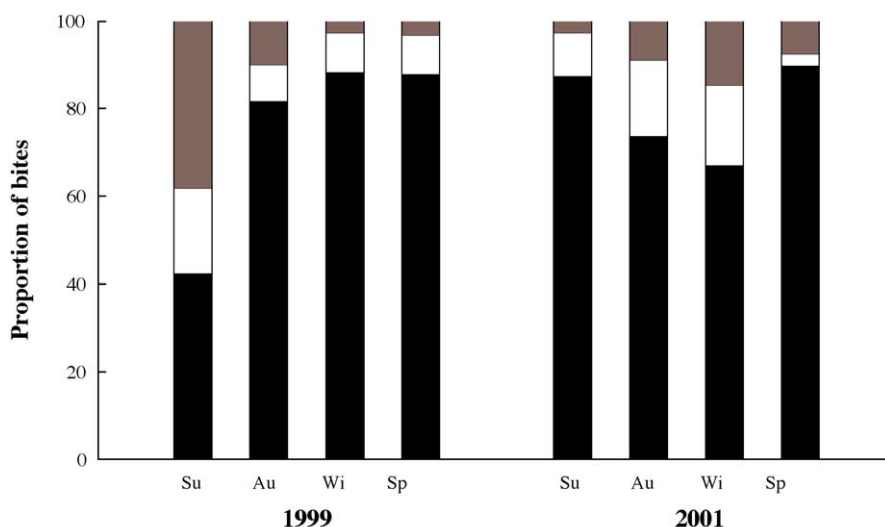


Fig. 3. The donkeys' diet composition, with its seasonal variation in 1999 and 2001. Black: proportion of bites taken of graminoids. White: proportion of bites taken of forbs. Grey: proportion of bites taken of woody plants. Su: summer, Au: autumn, Wi: winter, Sp: spring.

Table 5

Diet compositions of the donkeys when foraging in grassy habitat, scrub and woodland, in the various seasons and throughout the year in 1999 and 2001

Season	Habitat	1999				2001			
		Bites/6 h	%G	%F	%W	Bites/3 h	%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

Bites per 6 h (or 3 h): mean number of bites taken during a 6 h (or 3 h) observation session in each of the three habitat types. %G: proportion of bites taken of graminoids. %F: proportion of bites taken of forbs. %W: proportion of bites taken of woody plants.

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  $\times$  Habitat:  $F_{4,471} = 14.39$ ;  $p < 0.001$ ). Though, this result cannot be interpreted without attention for the significant interactions Class  $\times$  Habitat  $\times$  Season ( $F_{12,485} = 5.14$ ;  $p < 0.001$ ) and Class  $\times$  Habitat  $\times$  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  $\times$  Season  $\times$  Year, Class  $\times$  Year, Class  $\times$  Season and Class.

#### 4. Discussion

Little knowledge is available on the grazing behaviour of donkeys (Aganga and Tsopito, 1998; Canacoo and Avorny, 1998; Moehlman, 1998a,b), 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 and 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 than ponies, when fed ad libitum. Since voluntary food consumption is proportional to metabolic rate (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.

#### 4.1. 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 and Hoffmann, 2004), while Shetland ponies grazed 71% of their daytime (Lamoot et al., 2005) and Konik horses spend 73% of the period between 6 h and 24 h 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 3 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 h in 1998 up to 10 min/6 h in 2000, remaining though a low time investment and can therefore 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 and Balph, 1987, 1988). We suppose that this phenomenon appears even more strongly 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, 1992; Pratt et al., 1986; Berger et al., 1999; Cosyns et al., 2001; Menard et al., 2002), as well as in subarctic conditions (Salter and Hudson, 1979). Those authors investigating foraging behaviour in spring as well, found foraging times in spring comparable to those in winter (Duncan, 1985, 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 (unpublished 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 g/m<sup>2</sup>, 205 g/m<sup>2</sup>, 196 g/m<sup>2</sup> and 177 g/m<sup>2</sup> in summer, autumn, winter and spring, respectively. Life 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 suppose that the high 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.

#### 4.2. *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 3 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 and 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 the ponies remained on a diet of graminoids and forbs, and did not browse (Lamoot et al., 2005).

The increased use of scrub and woodland during autumn and winter coincides with a general decline in (life) biomass of the grassy vegetation units (unpublished 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 and 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 unit with relatively high biomass; unpublished data Cosyns) after 3 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., *C. 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 (Vervaeet, 2002). This definitely indicates that grass biomass availability declined severely in this relatively productive grassy vegetation unit. Since *C. 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 units. The increased use of rough vegetation in 2000 compared to 1998 can be a result of this. It might also explain at least partly the increased use of scrub in autumn 2000 (37% of the grazing time) as *C. epigejos* is still an important forage in autumn, though 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. In addition, we 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.

#### 4.3. 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 and Tsopito, 1998). Our data of 2001 showed a similar trend in the "Houtsaegeerduinen", with an increased browsing activity in autumn and winter. In 1999, the donkeys browsed most in summer when they foraged selectively on fruits of *R. pimpinellifolia*, though this consumption of

fruits cannot really be considered as a 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%, woody plants: 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., 2005). 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 and 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.

#### 4.4. 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 *U. dioica*, locally very abundant in the woodland undergrowth. In Botswana the donkeys peeled the bark of trees when there was food scarcity (Aganga and 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 donkeys' menu as well. They consumed leaves and branches of *Acer pseudoplatanus*, *Fraxinus excelsior*, *Populus alba*, *U. minor*, *A. 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%). *L. 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*.

#### 4.5. A role in nature management

Grazing management has been implemented in the “Houtsaegeerduinen” to prevent the expansion of dominant grass species like *C. epigejos* and *A. elatius* and the expansion of dense scrubs of *Hippophae rhamnoides* and *L. 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, *C. epigejos* is the main graminoid species of their diet (32% in 1999; 19% in 2001) (Table 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 (Vervaeke, 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 (unpublished 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. *L. vulgare*, which is browsed intensively from autumn till spring, becomes visibly less vital when growing in accessible places, e.g., at scrub edges. *H. 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 *H. 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, 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., 2005).

Another question related to the introduction of the donkeys as a management tool is whether they are able to cope with such 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 loss of condition during the winter period (unpublished data Cosyns). Mean weight data of five adult mares was  $180 \pm 8$  kg on 04/05/2000, was  $166 \pm 15$  kg on 21/03/2001 and was  $179 \pm 23$  kg on 23/10/2001. 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 stable condition. The analyses of the blood samples, taken yearly from all the individuals, showed that the donkeys did not perform 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.

## 5. Conclusions

We conclude that the donkeys have a similar time budget as other free-ranging equids, with grazing as the main time investment. Over a period of 3 years we found a trend of decreasing grazing times and increasing resting times, suggesting an increasingly efficient foraging behaviour. Both habitat use and diet composition are variable over time. The grassy habitat is highly preferred in all seasons, though a minor shift appears to scrub and woodland in autumn and winter. Further research is needed to compare both the foraging behaviour and the impact of donkeys on coastal dune vegetation, with other large herbivores. Though, it seems that donkeys can play a role in nature management in ecosystems providing only low forage quality and quantity.

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## References

- Aganga, A.A., Tsopito, C.M., 1998. A note on the feeding behaviour of domestic donkeys: a Botswana case study. *Appl. Anim. Behav. Sci.* 235–239.
- Altmann, J., 1974. Observational study of behaviour: sampling methods. *Behaviour* 49, 227–267.
- Bauer, I.E., McMorrow, J., Yalden, D.W., 1994. The historic range of three equid species in north-east Africa: a quantitative comparison of environmental tolerances. *J. Biogeography* 21, 169–182.
- Berger, A., Scheibe, K.-M., Eichhorn, K., Scheibe, A., Streich, J., 1999. Diurnal and ultradian rhythms of behaviour in a mare group of Przewalski horse (*Equus ferus przewalskii*), measured through one year under semi-reserve conditions. *Appl. Anim. Behav. Sci.* 64, 1–17.
- Canacoo, E.A., Avornyo, F.K., 1998. Daytime activities of donkeys at range in the coastal savanna of Ghana. *Appl. Anim. Behav. Sci.* 60, 229–234.
- Cosyns, E., Degezelle, T., Demeulenaere, E., Hoffmann, M., 2001. Feeding ecology of Konik horses and donkeys in Belgian coastal dunes and its implications for nature management. *Belg. J. Zool.* 131, 111–118.
- Cuddeford, D., Pearson, R.A., Archibald, R.F., Muirhead, R.H., 1995. Digestibility and gastro-intestinal transit time of diets containing different proportions of alfalfa and oat straw given to Thoroughbreds, Shetland ponies, Highland ponies and donkeys. *Anim. Sci.* 61, 407–417.
- Duncan, P., 1983. Determinants of the use of habitat by horses in a Mediterranean wetland. *J. Anim. Ecol.* 52, 93–109.

- Duncan, P., 1985. Time budgets of Camargue horses. III. Environmental influences. *Behaviour* 92, 188–208.
- Duncan, P., 1992. Horses and grasses: the nutritional ecology of equids and their impact on the Camargue. *Ecological Studies*, vol. 87. Springer Verlag, New York, pp. 287.
- Gordon, I.J., 1989a. Vegetation Community Selection by ungulates on the Isle of Rhum. II. Vegetation community selection. *J. Appl. Ecol.* 26, 53–64.
- Gordon, I.J., 1989b. Vegetation community selection by ungulates on the Isle of Rhum. III. Determinants of vegetation community selection. *J. Appl. Ecol.* 26, 65–79.
- Gordon, I.J., Illius, A.W., 1989. Resource partitioning by ungulates on the Isle of Rhum. *Oecologia* 79, 383–389.
- Illius, A.W., Gordon, I.J., 1993. Diet selection in mammalian herbivores: constraints and tactics. In: Hughes, R.N. (Ed.), *Diet Selection. An Interdisciplinary Approach to Foraging Behaviour*. Blackwell, Oxford, pp. 157–181.
- Izraely, H., Choshniak, I., Shkolnik, A., 1994. Dehydration and rehydration in donkeys: the role of the hind gut as a water reservoir. *J. Basic Clin. Physiol. Pharmacol.* 5, 89–100.
- Izraely, H., Choshniak, I., Stevens, C.E., Demment, M.W., Shkolnik, A., 1989. Factors determining the digestive efficiency of the domesticated donkey (*Equus asinus asinus*). *Q. J. Exp. Physiol.* 74, 1–6.
- Jacobs, J., 1974. Quantitative measurement of food selection. A modification of the Forage Ratio and Ivlev's Electivity Index. *Oecologia* 14, 413–417.
- Lamoot, I., Hoffmann, M., 2004. Do season and habitat influence the behaviour of Haflinger mares in a coastal dune area? *Belg. J. Zool.* 134, 97–103.
- Lamoot, I., Meert, C., Hoffmann, M., 2005. Habitat use of ponies and cattle foraging together in a coastal dune area. *Biol. Conserv.* 122, 523–536.
- McCarthy, G., 1998. *Practical Horse and Pony Nutrition*. J.A. Allen & Co. Ltd., London, p. 263.
- Menard, C., Duncan, P., Fleurance, G., Georges, J.-Y., Lila, M., 2002. Comparative foraging and nutrition of horses and cattle in European wetlands. *J. Appl. Ecol.* 39, 120–133.
- Moehlman, P.D., 1998a. Behavioral patterns and communication in feral asses (*Equus africanus*). *Appl. Anim. Behav. Sci.* 60, 125–169.
- Moehlman, P.D., 1998b. Feral asses (*Equus africanus*): intraspecific variation in social organization in arid and mesic habitats. *Appl. Anim. Behav. Sci.* 171–195.
- Owen-Smith, N., 1994. Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology* 75, 1050–1062.
- Pearson, R.A., Archibald, R.F., Muirhead, R.H., 2001. The effect of forage quality and level of feeding on digestibility and gastrointestinal transit time of oat straw and alfalfa given to ponies and donkeys. *Br. J. Nutr.* 85, 599–606.
- Pratt, R.M., Putman, R.J., Ekins, J.R., Edwards, P.J., 1986. Use of habitat by free-ranging cattle and ponies in the New Forest, Southern England. *J. Appl. Ecol.* 23, 539–557.
- Provenza, F.D., Balph, D.F., 1987. Diet learning by domestic ruminants: theory, evidence and practical implications. *Appl. Anim. Behav. Sci.* 18, 211–232.
- Provenza, F.D., Balph, D.F., 1988. The development of dietary choice in livestock on rangelands and its implications for management. *J. Anim. Sci.* 66, 2356–2368.
- Provoost, S., Ampe, C., Bonte, D., Cosyns, E., Hoffmann, M., 2002. Ecology, management and monitoring of dune grassland in Flanders, Belgium. In: Veloso-Gomes, F., Taveira-Pinto, F., das Neves, I., (Eds.), *The Changing Coast, Rapportnummer 2*, Porto, Portugal, pp. 11–20.
- Putman, R.J., Pratt, R.M., Ekins, J.R., Edwards, P.J., 1987. Food and feeding behaviour of cattle and ponies in the New Forest, Hampshire. *J. Appl. Ecol.* 24, 369–380.
- Rittenhouse, L.R., 1986. The relative efficiency of rangeland use by ruminants and non-ruminant herbivores. In: Gudmundsson, O. (Ed.), *Grazing Research at Northern Latitudes*. Plenum Press, New York, pp. 179–191.
- Salter, R.E., Hudson, R.J., 1979. Feeding Ecology of Feral Horses in Western Alberta. *J. Range Manage.* 32, 221–225.
- Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E., Swift, D.M., 1987. Large herbivore foraging and ecological hierarchies. *Bioscience* 37, 789–799.
- Stuth, J.W., 1991. Foraging behaviour. In: Heitschmidt, R.K., Stuth, J.W. (Eds.), *Grazing Management: an Ecological Approach*. Timber Press Inc., Portland, Oregon, pp. 65–83.

- van Dierendonck, M.C., Bandi, N., Batdorj, D., Dürgerham, S., Munkhtsog, B., 1996. Behavioural observations of reintroduced Takhi or Przewalski horses (*Equus ferus Przewalskii*) in Mongolia. *Appl. Anim. Behav. Sci.* 50, 95–114.
- Van Dyne, G.M., Brockington, N.R., Szocs, Z., Duek, J., Ribic, C.A., 1980. Large herbivore subsystem. In: Breymer, A.I., Van Dyne, G.M. (Eds.), *Grasslands, Systems Analysis and Man*. Cambridge University Press, Cambridge, pp. 269–537.
- Vervaet, H., 2002. Ontwikkeling van soortenrijk duingrasland uit door duinriet gedomineerde vegetatie: de rol van beheer, endozoöchorie en bodemzaadvoorraad. Universiteit Gent, Gent, p. 103.
- Vulink, T., 2001. Hungry herds. Management of temperate lowland wetlands by grazing, *Van Zee tot Land* 66, Lelystad, p. 394.
- Webster, A.J.F., 1985. Differences in the energetic efficiency of animal growth. *J. Anim. Sci.* 61 (Suppl. 2), 92–103.