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Is the different diet selection by sheep and donkeys a tool for the management of threatened sand vegetation?

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Abstract

Extensive grazing by ruminants and nonruminants is often used for managing fallow grassland in order to restore ecosystems with, in many cases, formerly high phytodiversity. Diet selection is a main component of total livestock impact on the plant species composition of the paddocks. Due to morphological and physiological differences, ruminants and nonruminants are expected to have different grazing preferences. We investigated stands of the *Armerio-Festucetum trachyphyllae* (*Koelerio-Corynephoretea*) in a dry and nutrient-poor inland sand ecosystem in the northern upper Rhine valley (Hesse). Sheep breeds (as a model for ruminants) and donkeys (as a model for nonruminants) were used as grazing animals. Additionally, we investigated the impact of successive combination of sheep/donkeys. Two different subtypes of the *Armerio-Festucetum* (each threefold replicated) were each grazed once a year for a short period. In 2003 and 2004 the effects of the three treatments (sheep grazing, donkey grazing and successive two-species grazing) on phytomass extraction were investigated in a field experiment. The weighed dry phytomass of the grazing-leftover on 2-m² plots was compared with that on mini-exclosures of the same size, differentiated into the three plant functional types (PFTs) "graminoids", "legumes" and "other herbs"

The maximum phytomass extraction was achieved with the two-species approach and no differences between the total quantitative phytomass extraction by either sheep or donkeys could be detected. Concerning the PFTs, sheep extracted more phytomass of herbs than of graminoids, whereas donkeys selected for legumes. With the two-species treatment all PFTs were grazed to the same degree. – It is concluded that especially due to the high phytomass extraction and the complementary use of graminoids, herbs and legumes in the case of the multispecies approach, this treatment is best suited for the management of ruderalised sites.

Zusammenfassung: Kann die verschiedenartige Nahrungswahl von Schafen und Eseln für eine optimale Pflege gefährdeter Sandvegetation genutzt werden?

Extensive Beweidung durch Wiederkäuer und Nicht-Wiederkäuer wird oft als Management-Methode für brachliegendes Grasland eingesetzt, um den in vielen Fällen einst hohen Artenreichtum dieser Systeme zu renaturieren. Die Pflanzenarten-Zusammensetzung auf den Weidekoppeln wird dabei hauptsächlich durch die Nahrungswahl der Weidetiere beeinflusst. Aufgrund der physiologischen Unterschiede ist davon auszugehen, dass Wiederkäuer und Nicht-Wiederkäuer unterschiedliche Nahrungspräferenzen haben. Wir untersuchten Bestände des *Armerio-Festucetum trachyphyllae* (*Koelerio-Corynephoretea*) in einem trockenen und nährstoffarmen Binnendünen-Gebiet der nördlichen Oberrheinebene (Hessen). Als Weidetiere wurden verschiedene Schafrassen (als Modell für Wiederkäuer) und Esel (als Modell für Nicht-Wiederkäuer) eingesetzt. Zusätzlich untersuchten wir die Auswirkungen sukzessiver Schaf-/Eselbeweidung. Zwei unterschiedliche Subtypen des *Armerio-Festucetum trachyphyllae* (jeder dreifach repliziert) wurden einmal im Jahr beweidet. In den Jahren 2003 und 2004 konnten die Phytomasse-Extraktionen der drei verschiedenen Beweidungstypen (Schaf, Esel, sukzessive Schaf-/Eselbeweidung) untersucht werden. Auf jeweils 2 m² großen Probeflächen verglichen wir die gewogene trockene Phytomasse des Weiderestes mit der Phytomasse von durch Draht-Weidekörbe geschützten Klein-Exclosures. Die Phytomasse wurde jeweils getrennt in die drei funktionellen Pflanzengruppen: „Grasartige", „Leguminosen" und „sonstige Kräuter" Der maximale Phytomasse-Entzug wurde im Fall der sukzessiven Schaf-/Eselbeweidung erzielt. Hinsichtlich der maximalen quantitativen Extraktion ließen sich keine Unterschiede zwischen Schaf- und Eselbeweidung feststellen. Bezogen auf die funktionellen Pflanzengruppen nutzten Schafe in stärkerem Maße „sonstige Kräuter", wohingegen Esel Leguminosen bevorzugten. Bei sukzessiver Schaf-/Eselbeweidung zeigte sich keine Präferenz gegenüber einer funktionellen Pflanzengruppe. – Es lässt sich rückschließen, dass im Fall von ruderalisierten Flächen die Multispecies-Beweidung aufgrund der hohen Phytomasse-Extraktion und der komplementären Nutzung der funktionellen Pflanzengruppen die am besten geeignete Methode ist.

Keywords: multispecies grazing, phytomass extraction, ruderalised site, ruminant, standing crop, weighed phytomass.

1. Introduction

During recent years, extensive grazing has turned out to be an important means of ecosystem management, used to restore phytodiversity (e. g. KOOIJMAN & VAN DER MEULEN 1996, HELLSTRÖM et al. 2003, SCHWABE et al. 2004, PYKÄLÄ et al. 2005). Besides other impacts which have been considered important for reaching goals of nature protection, e. g., the creation of gaps (BULLOCK et al. 1994, OLFF & RITCHIE 1998) or epizoochorous and endozoochorous transport (COSYNS 2004, EICHBERG et al. 2005, 2007, WESSELS et al. 2008), selective phytomass extraction is an important effect of livestock on plant species composition.

Depending on the ecosystem type, different species of livestock are used. Often ruminants, in most cases cattle or sheep but sometimes also goats, are of importance. In other cases, nonruminants, especially equids are used as grazing animals. Recently traditional multispecies grazing with a combination of ruminants and nonruminants has also been considered as a tool of ecosystem management (e. g. MENARD et al. 2002, LOUCOUGARAY et al. 2004, SÜSS 2004, LAMOOT et al. 2005b). In these cases, ruminants and nonruminants are often represented by cattle and horses for management of wet or moist ecosystems, but also for dune vegetation complexes (LAMOOT 2004, LAMOOT et al. 2005b). Whereas the feeding behaviour of equids is thought to be characterised by large intakes with low nutrient extraction (MUELLER et al. 1998), ruminants are said to possess a certain degree of "nutritional wisdom" (NGWA et al. 2000). Sheep diets can be even more variable than cattle diets (GRANT et al. 1985).

Especially species-rich grasslands on nutrient-poor soils have become rare in the last decades and often depend on management and restoration (e. g. KIEHL & PFADENHAUER 2007). Among the most threatened habitats in Central Europe, open base-rich inland sand ecosystems are known to depend on an extensive grazing impact (e. g. SCHWABE et al. 2004, SÜSS et al. 2004). Since 1995 we have studied sheep-grazed plots compared with ungrazed reference plots and elaborated a successional model (SÜSS et al. 2004, SCHWABE & KRATOCHWIL 2008). Most of our sand ecosystems in middle-successional stages are endangered by grass-encroachment (KOOIJMAN & VAN DER MEULEN 1996). To optimise their management, sheep grazing should be supplemented by other grazing animals to reduce monodominant stands of graminoids and in general the increase of ruderal species (e. g. of *Calamagrostis epigeios*) to a high extent. If high amounts of phytomass are extracted, low-competitive species will be favoured, e. g., because microsites are created (SÜSS 2005). To study the impact of different grazing animals we recorded the developments in permanent plots (443 plots à 25 m²) with different grazing regimes (SÜSS & SCHWABE 2007) in a 4-year study.

For a better understanding of the different components of the grazing impact, in the present study we report results obtained with a complementary approach: the direct diet selection and phytomass extraction by ruminants and nonruminants during single- and multispecies grazing of the *Armerio-Festucetum* (*Koelerio-Corynephoretea*). As this plant community is characterised by rather dry and nutrient-poor conditions, we chose sheep breeds (Skudde, Moorschnucke, Rhoen sheep) as grazing ruminants which can cope with these conditions. With reference to the dryness and the lack of nutrient-rich sites, equids were represented by donkeys in our case, reflecting their origin in a hot semiarid environment (PEARSON et al. 2001). LAMOOT et al. (2005a) stated that donkeys are sufficiently well nourished by the scarce vegetation of coastal sand ecosystems and might play a major role in nature management, especially in ecosystems with low forage quality. As yet there are only a few studies on donkeys as grazing animals (e. g. AGANGA & TSOPITO 1998, CANACOO & AVORNYO 1998, AGANGA et al. 2000, COSYNS et al. 2001, LAMOOT 2004, LAMOOT et al. 2005a) and no study has been done in a comparable, primarily calcareous inland sand ecosystem. The successive combination of sheep and donkeys was investigated in an additional multispecies approach.

Regarding the agroeconomical context, sheep in our investigation area are integrated in a system of direct marketing of high-quality meat from nature protection areas (MÄHRLEIN 2004), while donkeys are mainly used for breeding purposes and to assist public relations of a nature protection association.

We studied differences in quantitative phytomass extraction and differences in the quantitative reduction of the three plant functional types (PFTs) "graminoids", "legumes" and "other herbs" for sheep grazing, donkey grazing and successive sheep and donkey grazing. This was accompanied by a qualitative examination of the grazing preferences of these animals for the most frequent plant species. As far as we know, no comparable study in a high-phytodiversity ecosystem has yet been published.

Plant species composition and thus grazing extraction may be different in different years and vegetation types – for instance, according to climatic conditions (FAHNESTOCK & DETLING 1999). Furthermore, especially equids have a different foraging behaviour if they graze the same paddock several times, because they tend to avoid grazing at last years' faeces-accumulation sites (BOGNER & GRAUVOGL 1984). Therefore, and due to the impact of the annual differences in precipitation regime, the study was repeated in two successive years (2003 and 2004) in two closely related subtypes of the *Armerio-Festucetum.*

The main questions are:
1. How much phytomass is grazed in the case of sheep grazing, donkey grazing and successive sheep and donkey grazing?
2. Which PFTs are selected by sheep and donkeys and how intense is the phytomass extraction of these PFTs in case of the two-species treatment? Which plant species are grazed, and which are rejected by both livestock species?
3. Are there different results depending on the year of investigation and/or on the vegetation type?

2. Study area and grazing animals

2.1. Study area

The investigation took place in the years 2003 and 2004 in the northern upper Rhine valley (Germany) about 30 km south of Frankfurt/Main (Hesse) near Darmstadt. A nature reserve ("Ehemaliger August-Euler-Flugplatz"), 71 ha in size, served as a model area for grazed inland sand ecosystems. The drifted sand had been blown-out from primary calcareous Rhine deposits during late glacial and postglacial periods. Especially in the eastern part of the investigation area calcareous substrate is represented. In the central and western parts of the area primarily base-rich sands in the topsoil have been progressively acidified due to successional processes. The investigation site is characterised by plant communities belonging to the *Armerio-Festucetum*. The *Armerio-Festucetum typicum* is restricted to more consolidated conditions, partial decalcification in the upper soil, and is characterised by the typical plant species *Medicago falcata + x varia* and *Bromus hordeaceus* while the floristically closely related *Festuca duvalii*-subtype is characterised by more open and base-rich sites with a higher presence of *Festuca duvalii* and *F. trachyphylla* and, e. g., *Ononis repens*.

We use the name *Armerio-Festucetum trachyphyllae* (Libbert 1933) Knapp 1948 ex Hohenester 1960 according to OBERDORFER (1978), see also FAUST et al. (2007).

To prevent succession and grass-encroachment, the whole area has been grazed by sheep since 1999 (SCHWABE et al. 2002). Parts of the area have been grazed by donkeys since 2002 and successive sheep and donkey grazing started in 2003.

The weather conditions in the two investigated years were very different. As the grazing period of the investigated paddocks always finished in August and the first months of the year are important for the development of annual plant species, the mean climate values from January to August of 2003 and 2004 are given. The mean temperature was 12.9°C (data from Frankfurt/Main airport [DEUTSCHER WETTERDIENST, Internet]) in 2003 and 11.7°C in 2004 (long-term average for these months: 12.0°C). Duration of sunshine was 1652 h, or 1239 h, respectively (long-term average: 1342 h) and the total precipitation reached 230 mm in 2003 and 410 mm in 2004 (long-term average: 390 mm). Thus 2003 was characterised by a very high duration of sunshine in combination with low precipitation rates in comparison to long-term average values, whereas 2004 was more or less an average year.

2.2. Grazing animals

Sheep and donkeys, as models for ruminants and nonruminants, are well adapted to dry and nutrient-poor conditions. Due to morphological and physiological differences between the species, e. g. the structure of the incisor arcade or different digestive systems, they are in different ways appropriate grazers of the investigated ecosystem and differences in foraging behaviour and habitat use are expected (LAMOOT et al. 2005b).

Selective grazing has been documented for sheep (HAFEZ 1962, STROH et al. 2002, 2007, HÜLBER et al. 2005) as well as for donkeys (LEGEL 1993, MUELLER et al. 1998, COSYNS et al. 2001), so that it is possible that the grazed areas include less preferred species. But only sheep are said to be able to select for nutrient-rich plants on paddocks that are characterised by lower mean nutrient values (JEROCH et al. 1999). The ability to cope with a nutrient-poor diet depends on the sheep breed (BARTOLOMÉ et al. 1998, JEROCH et al. 1999). Sheep grazing is often used for nature conservation and has proved to be an adequate management method (JEROCH et al. 1999, HELLSTRÖM et al. 2003).

As hindgut fermenters equids are able to cope with a diet having a high fibre content (JEROCH et al. 1999, MENARD et al. 2002) and can consume fibre at a faster rate than ruminants (MUELLER et al. 1998). As is generally known, in contrast to ruminants, equids have upper and lower incisors and mobile lips; thus they can graze close to the ground and consume short vegetation efficiently (AGANGA & TSOPITO 1998, JEROCH et al. 1999, AGANGA et al. 2000). It is specific for equids that faeces-sites are not grazed (BOGNER & GRAUVOGL 1984, LOUCOUGARAY et al. 2004). In the case of multispecies grazing with ruminants, this effect may be compensated (JEROCH et al. 1999).

3. Materials and methods

3.1. Experimental design and phytomass sampling

In both vegetation types (*Armerio-Festucetum trachyphyllae typicum* and *Festuca duvalii*-subtype) 9 homogeneous paddocks each measuring approx. 700 m² were chosen. In accordance with the practicability of the grazing regime the three treatments (sheep grazing, donkey grazing, successive sheep and donkey grazing) were assigned to three paddocks each. So for each vegetation type, the investigation was replicated thrice. Sampling was carried out in 2003 and 2004 on the same paddocks. In each paddock 5 (2003) or 4 (2004) mini-exclosures (metal baskets) with an area of 1 m x 2 m were established prior to grazing to assess the percentage of grazed phytomass. Their location was determined by evaluating how best to represent the various vegetational subtypes in the paddocks. The positions were different in the two years. At every ungrazed mini-exclosure plot and an adjacent complementary grazed plot of the same size, the vascular plant species were recorded by relevés according to the scale of BARKMAN et al. (1964) before grazing took place. Cryptogams were not sampled by the harvest method (see below) and therefore are only mentioned in Section 4.1. They are included in our 4-year permanent-plot study (SÜSS & SCHWABE 2007) in the same area. Nomenclature follows WISSKIRCHEN & HAEUPLER (1998).

Immediately after grazing of each paddock, the ungrazed plots and the grazing-leftover on the grazed plots were mown by an electric clipper up to a stubble-field height of about 2 cm, and the phytomass – separated into the groups "graminoids" (including *Carex hirta*), "legumes" and "other herbs" (without legumes) – was dried for 48 h at 70°C and afterwards weighed. The percentage of grazed phytomass for each plant group as well as for the total phytomass of each plot was calculated as 100 % * [$\text{phytomass}_{(\text{ungrazed plot})}$ – $\text{phytomass}_{(\text{grazed plot})}$] / $\text{phytomass}_{(\text{ungrazed plot})}$.

In case of very small phytomass samples of one PFT at the ungrazed plot, it is not certain whether an even smaller complementary sample at the corresponding grazed plot has indeed been grazed selectively or grazed "by accident" because, for example, a small herb was imbedded within a bulk of grasses. Therefore PFTs with less than 10 g dry phytomass were not taken into account for the differentiated analysis.

Additionally, the grazing preferences of the animals on the level of plant species were estimated for each pair mini-exclosure/complementary ungrazed plot as follows. Immediately after grazing, the apparent grazing intensity was assessed by the modified scale of STROH et al. (2002): not/hardly grazed (0 %–5 % of phytomass grazed), grazed (6 %–50 %) and intensively grazed (> 50 %). All results (both years, both vegetation types) were pooled for each plant species and the median grazing preference was calculated for sheep and donkeys.

3.2. Grazing regime

The paddocks were grazed during summer (mainly in June). The sheep grazing regime was a dynamic one with approximately 500 sheep grazing small areas of about 1 ha for only 1 or 2 days. The above-mentioned paddocks where the investigation took place were integrated in these areas. In case of donkey grazing, 2–3 adult donkeys and one foal grazed the approximately 700-m² paddocks for about 3–5 days, depending on the amount of phytomass. For sheep as well as for donkey grazing, the paddocks were grazed as long as an adequate food supply for the animals could be guaranteed. With the successive sheep and donkey grazing regime, the paddocks were grazed by sheep as long as the sheep found adequate food resources. Afterwards (about 1 to 5 days later), the grazing-leftover of the sheep was grazed by the donkeys, in this case for 1–2 days.

3.3. Statistical analyses

The impacts of the factors "animal", "year", "vegetation type" and "plant functional type" on the phytomass extraction were analysed by means of mixed linear models (SAS 8.02, Proc Mixed). These models allow a comparison of the goodness of fit of several covariance structures and are therefore especially suitable for analysing repeated-measures data (LITTELL et al. 1998). Usually when comparing the several measurements on the same plot, data close in time are more highly correlated than measures far apart in time. A number of different covariance structures can be modelled and compared by SAS. We tested autoregressive (1), heterogeneous autoregressive (1), autoregressive moving averages (1,1), unstructured, compound symmetry and Huynh-Feldt covariance structure as suggested by LITTEL et al. (1998) and UCLA Academic Technology Services (Internet). The structure with the best goodness of fit (Akaike information criterion, AIC) was chosen for final calculations. These structures were: heterogeneous autoregressive for the analysis of the available phytomass and unstructured for the analyses of the percentage of grazed phytomass in total or PFT phytomass. The standard errors given here are those resulting from the Proc Mixed analysis. Tukey-adjustment was used for post hoc multiple comparisons.

4. Results

4.1. Floristic structure of the plots and phytomass of the ungrazed plots

In total in both years and all plots, 58 vascular plant species were recorded, 51 in the *Armerio-Festucetum typicum* and 42 in the *Festuca duvalii*-subtype. Additionally, 6 cryptogam species (the mosses *Brachythecium albicans, Hypnum cupressiforme* var. *lacunosum* and *Tortula ruraliformis* and the lichens *Cladonia furcata* agg., *Cladonia rangiformis* and *Peltigera rufescens*) were present but not harvested (and therefore not recorded in the relevés), because they grow below the stubble level. We show the floristic structure of the two subtypes in Table 1 for the year 2004 (with average weather conditions) by the example of the harvested mini-exclosures. Apart from *Festuca duvalii*, this subtype is characterised by higher presence of some pioneer species (e.g., *Medicago minima, Trifolium arvense*) and negatively by lack or low presence of species which reflect more consolidated, often slightly ruderalised conditions. These species (*Elymus repens, Achillea millefolium, Cerastium arvense* and others) are mainly restricted to the "*typicum*" Table 1 shows that the plots representing the different treatments (donkeys, sheep, sheep + donkeys) are comparable within the F- resp. A-paddock in their floristic structure. By means of the mini-exclosures the phytomass of the ungrazed plots was assessed in order to provide a background for the following analyses. The effects of the variables "year", "plant functional type", "animal" and "vegetation type" on the phytomass were analysed by a mixed linear model. The results are shown in Table 2. The differences between the two vegetation types are not significant but there is a significant interaction "year*PFT" and "animal*year", so Fig. 1 gives the detailed composition of PFTs for both years and all three treatments.

Generally, phytomass was higher in 2004 than in 2003. This increase is expressed by a marked augmentation of herbs (x 6.6) and legumes (x 2.9), whereas graminoids decreased (x 0.8). As a consequence, graminoids accounted for ca. 75 % of the phytomass in 2003 but only for 37 % in 2004. Because for this analysis the ungrazed plots were used, the weak significance of the factor "animal" is not a treatment effect but an a priori difference in the

Table 1: Floristic structure of the mini-exclosure plots (each 1 m x 2 m) as an example for the two subtypes of the *Armerio-Festucetum* in the year 2004 (presence values in %). Red List species for Hesse are marked with R.

F: *Armerio-Festucetum, Festuca duvallii*-subtype, A: *typicum*, d: relevé on donkey-grazed paddock, s: on sheep-grazed paddock, s+d: on sheep- and donkey-grazed paddock (to show comparability between paddocks).

Tab. 1: Floristische Struktur der Klein-Weideausschlussflächen (je 1 m x 2 m) als Beispiel für die zwei Subtypen des *Armerio-Festucetum* im Jahr 2004 (Stetigkeiten in %). Arten der Roten Liste Hessen sind mit R markiert.

F: *Armerio-Festucetum, Festuca duvallii* Subtyp, A: *typicum*, d: Aufnahmen auf Esel-beweideten Koppeln, s: auf Schaf-beweideten Koppeln, s+d: auf Schaf- und Esel-beweideten Koppeln (nur zum Beleg der Vergleichbarkeit der Koppeln).

		F	F	F	A	A	A
	community subtype	F	F	F	A	A	A
	paddock type	d	s+d	s	d	s+d	s
	number of relevés	12	12	12	12	12	12
	mean number of species	9.9	8.7	7.6	16.3	13.4	11.7
	standard error	0.36	0.28	0.53	0.90	0.60	0.71
Koelerio-Corynephoretea species							
R	Koeleria macrantha	92	75	83	75	100	92
	Arenaria serpyllifolia	17	50	42	50	50	33
R	Armeria mar. ssp. elongata	50	42	33	67	42	25
	Erodium cicutarium	33	33	67	50	92	50
R	Medicago minima	17	67	67	42	25	50
	Trifolium arvense	75	25	17	8	25	25
	Trifolium campestre	58	33	17	58	42	33
	Echium vulgare	25	33	25	.	8	17
	Potentilla argentea	42	25	17	75	42	.
	Rumex acetosella	33	8	8	33	25	.
*R	Festuca duvalii/trachyphylla/ovina agg.	.	25*	58*	75	58	25
	Petrorhagia prolifera	17	17	.	8	.	8
	Sedum acre	17	.	17	17	17	.
R	Silene conica	8	.	.	8	.	.
R	Vicia lathyroides	.	.	.	50	.	.
Festuco-Brometea species							
	Centaurea stoebe	58	8	.	33	58	83
	Ononis repens	.	33	42	.	25	.
	Euphorbia cyparissias	.	17	17	.	8	.
R	Silene otites	.	.	.	8	.	.
d more consolidated and slightly ruderalised stands							
	Elymus repens	8	.	8	42	8	83
	Achillea millefolium	8	8	.	17	25	.
	Cerastium arvense	8	.	8	50	25	.
	Plantago lanceolata	17	.	.	42	33	25
	Crepis capillaris	.	8	.	25	17	8
	Carduus nutans	.	17	.	67	50	.
	Bromus hordeaceus	.	.	.	58	75	100
	Convolvulus arvensis	.	.	.	25	17	25
	Geranium molle	.	.	.	100	75	75
	Veronica arvensis	.	.	.	58	8	.
	Cynodon dactylon	.	.	.	8	42	.
Other species							
	Carex hirta	42	17	8	25	8	8
	Poa angustifolia	75	100	58	67	83	92
	Berteroa incana	17	25	8	83	83	100
	Silene latifolia ssp. alba	50	17	8	33	8	42
	Sisymbrium altissimum	8	17	8	42	8	33
	Verbascum phlomoides	67	67	42	50	25	8
	Medicago falcata + x varia	67	58	58	92	100	100
	Conyza canadensis	33	8	.	17	.	.
	Vulpia myuros	8	.	17	.	.	8
	Polygonum aviculare	.	.	8	17	.	8

Bromus tectorum	8	.	8	.	.	.
Oenothera biennis	8	.	.	.	8	.
Bromus inermis	.	25	8	.	.	.
Asparagus officinalis	.	.	.	8	8	.
Saponaria officinalis	.	.	.	8	8	.
Tragopogon dubius	17	.	.	.	.	.
Psyllium arenarium	8	.	.	.	.	.
Rumex thyrsiflorus	.	8	.	.	.	.
Capsella bursa-pastoris	.	.	.	25	.	.
Chenopodium album agg.	.	.	.	8	.	.
Lactuca serriola	.	.	.	.	8	.
Silene vulgaris	.	.	.	.	.	8

* R Festuca duvalii dominant

Table 2: Result of the SAS mixed-linear-model analysis of the available phytomass at the mini-exclosure plots. Significant effects are shown in bold print.
Num df: degrees of freedom Numerator, Den df: degrees of freedom Denominator, p: level of significance.

Tab. 2: Ergebnis der Analyse gemischt linearer Modelle für die verfügbare Phytomasse innerhalb der Mini-Exclosure-Flächen. Signifikante Ergebnisse sind fett gedruckt.
Num df: Freiheitsgrade des Numerators, Den df: Freiheitsgrade des Denominators, p: Signifikanzniveau.

effect	Num df	Den df	F Value	p
year	**1**	**12**	**33.57**	**<0.0001**
animal	**2**	**12**	**5.53**	**0.0199**
animal*year	**2**	**12**	**4.91**	**0.0277**
plant functional type (PFT)	**2**	**24**	**22.93**	**<0.0001**
year*PFT	**2**	**17**	**25.83**	**<0.0001**
animal*PFT	4	24	1.41	0.2592
animal*year*PFT	4	17	1.00	0.4358
vegetation type	1	12	1.22	0.2912
year*vegetation type	1	12	2.23	0.1614
animal*vegetation type	2	12	0.51	0.6127
animal*year*vegetation type	2	12	2.80	0.1006
vegetation type*PFT	2	24	3.23	0.0572
year*vegetation type*PFT	2	17	1.98	0.1683
animal*vegetation type*PFT	4	24	0.76	0.5605
animal*year*vegetation type*PFT	4	17	2.01	0.1393

paddocks. On the paddocks with mixed grazing, the phytomass was somewhat higher in both years, but the composition was similar to that on the sheep and donkey paddocks. In the following only the percentages of grazed phytomass are considered, so that the slight differences among the paddocks do not interfere with these analyses.

4.2. Phytomass extraction

In Fig. 2 the difference between sheep-grazed and -ungrazed areas for a dominance stand of the ruderal species *Berteroa incana* can be seen. Table 3 shows the result of the mixed-linear-model analysis of the relative phytomass extraction by the animals, not separated into different PFTs. The significance of the interaction-term "animal*vegetation type" demonstrates that differences in the experimental treatment ("animal") are dependent on the vegetation type but not on the year – despite the marked difference of the phytomass of ungrazed plots between 2003 and 2004 (see Table 2). As Fig. 3 shows, the *Festuca duvalii*-subtype is slightly grazed by sheep but significantly more intensively by the combination of sheep and donkeys. After Tukey-adjustment, the difference between sheep and donkeys is slightly not significant (p=0.06). Concerning the *Armerio-Festucetum trachyphyllae typicum*,

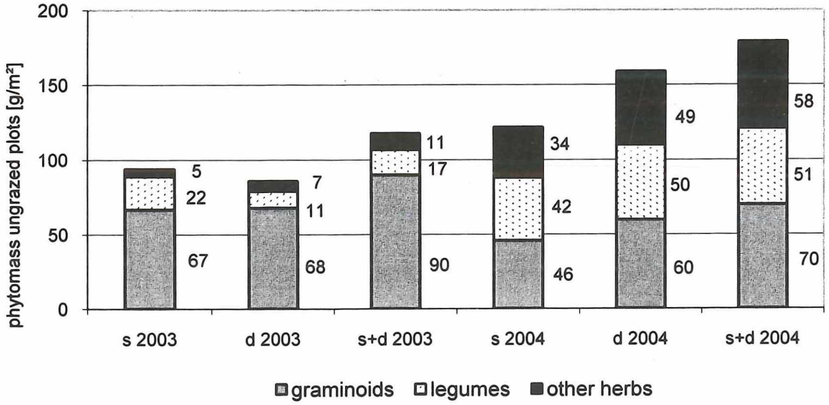

Fig. 1: Phytomass composition of the mini-exclosure plots for the three grazing regimes in 2003 and 2004. s: sheep, d: donkeys, s+d: successive sheep and donkey grazing.

Abb. 1: Phytomasse-Zusammensetzung der Mini-Exclosure-Flächen für die drei Weideregimes in den Jahren 2003 und 2004. s: Schafe, d: Esel, s+d: sukzessive Schaf-/Eselbeweidung.

Fig. 2: The picture shows the difference between sheep-grazed (left) and -ungrazed (right) areas for a dominance stand of the ruderal species *Berteroa incana* in the *Armerio-Festucetum trachyphyllae*. The non-grazed areas were protected by use of metal baskets (July 2004).

Abb. 2: Das Bild zeigt die Unterschiede zwischen Schaf-beweideten (links) und unbeweideten (rechts) Bereichen für einen Dominanzbestand der Ruderalart *Berteroa incana* innerhalb des *Armerio-Festucetum trachyphyllae*. Die nicht-beweideten Untersuchungsflächen wurden durch Weidekörbe aus Metall geschützt (Juli 2004).

Table 3: Result of the SAS mixed-linear-model analysis of the percentage of grazed phytomass. Significant effects are shown in bold print.
Num df: degrees of freedom Numerator, Den df: degrees of freedom Denominator, p: level of significance.

Tab. 3: Ergebnis der Analyse gemischt linearer Modelle für den prozentualen Phytomasse-Entzug. Signifikante Ergebnisse sind fett gedruckt.
Num df: Freiheitsgrade des Numerators, Den df: Freiheitsgrade des Denominators; p: Signifikanzniveau.

effect	Num df	Den df	F Value	p
year	1	12	0.13	0.7238
animal	**2**	**12**	**8.78**	**0.0045**
year*animal	2	12	2.15	0.1598
vegetation type	1	12	3.27	0.0958
year*vegetation type	1	12	0.00	0.9833
animal*vegetation type	**2**	**12**	**7.17**	**0.0089**
year*animal*vegetation type	2	12	0.06	0.9451

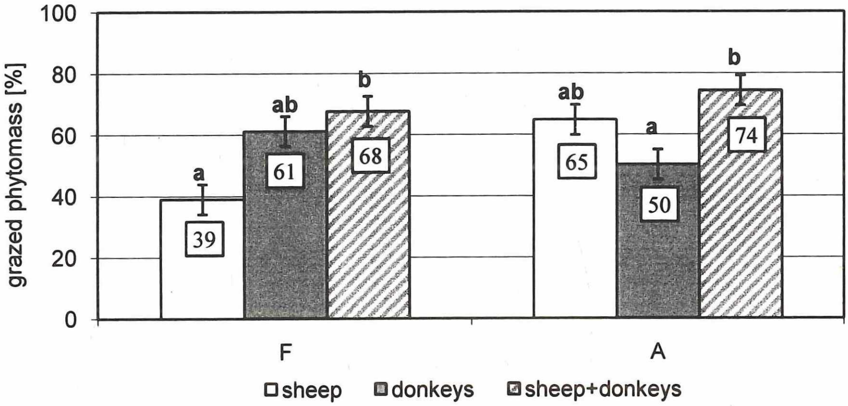

Fig. 3: Mean total phytomass extraction for the three grazing approaches and both vegetation types. Error: Standard error. A: *Armerio-Festucetum trachyphyllae typicum*, F: *Festuca duvalii*-subtype. a, b: average values within one vegetation type that are marked with different letters are significantly different.

Abb. 3: Mittlere Phytomasse-Extraktion für die drei Weideregimes und beide Vegetationstypen. Fehlerbalken: Standardfehler. A: *Armerio-Festucetum trachyphyllae* typicum, F: *Festuca duvalii*-subtype. a, b: Die mit unterschiedlichen Buchstaben markierten Mittelwerte innerhalb eines Vegetationstyps unterscheiden sich signifikant.

phytomass extraction by donkeys was significantly less than by successive sheep and donkey grazing, whereas the phytomass extraction of the sheep does not differ significantly from other treatments. Only in the case of sheep grazing could a significant difference between the percentage of grazed phytomass of the two vegetation types be ascertained, with a higher phytomass extraction in the *Armerio-Festucetum trachyphyllae typicum*.

4.3. Phytomass extraction of different PFTs and preferences for different plant species

To elucidate the dietary preferences of the animals on the level of the three PFTs "graminoids", "legumes" and "other herbs", a mixed linear model was calculated with four independent factors. According to the vegetation relevés the most frequent species of these PFTs were *Poa angustifolia* (graminoids), *Medicago falcata + x varia* (legumes) and *Berteroa incana* (other herbs). Table 4 shows the results of the analysis. Since the highest-order interaction term "animal*year*vegetation type*PFT" is significant, the interpretation has to be differentiated. Fig. 4 and Table 5 display the percentage of grazed phytomass for each combination of factors. In Fig. 5 mean values for the interaction "animal*PFT" have been calculated to show the most important results.

First, we specify the phytomass extraction by sheep. They utilised "other herbs" (79 %) more than graminoids (47 %). The low phytomass extraction of graminoids is very distinct in 2003 in the *Festuca duvalii*-subtype. While legumes usually occupy an intermediate position, in 2004 in the *Armerio-Festucetum trachyphyllae typicum* the grazing intensity on legumes was highest. In both years, more phytomass of legumes was consumed in the *Armerio-Festucetum trachyphyllae typicum* than in the *Festuca duvalii*-subtype. While in the first vegetation type, *Medicago falcata + x varia* is the most frequent legume, in the latter one *Ononis repens* is of greater importance. As demonstrated in Table 6, sheep prefer *Medicago falcata + x varia* to *Ononis repens.*

Second, we describe the results regarding donkey grazing. Out of the PFTs, legumes received the greatest percent utilisation by donkeys (76 %). Only in 2003 in the *Armerio-Festucetum trachyphyllae typicum* did they mainly extract "other herbs". The difference in phytomass extraction between "other herbs" (55 %) and graminoids (54 %) is negligible and not significant. Concerning plant species, also donkeys strongly prefer *Medicago falcata + x varia* to *Ononis repens;* the latter almost remained ungrazed.

In total, 38 plant species were grazed or intensively grazed: 27 by donkeys (6 graminoid species, 4 legumes and 17 other herbs) and 30 by sheep (7 graminoids, 6 legumes and 17 other herbs). 19 plant species were grazed by both animals, which is an overlap of 50 % (Table 6). The dominant graminoid species *Elymus repens, Carex hirta, Poa angustifolia* and *Cynodon dactylon* were grazed by donkeys as well as by sheep. The endangered plant species *Armeria maritima* ssp. *elongata, Medicago minima, Koeleria macrantha* and *Silene conica* are grazed by sheep as well as by donkeys.

As a consequence, the combined grazing resulted in a very homogeneous and high grazing impact on all PFTs and no significant differences between legumes (84 %), "other herbs" and graminoids (71 %) can be detected. Exceptional is the low grazing intensity, especially of herbs, in 2004 in the *Festuca duvalli*-subtype; here the most frequent herbal species was *Verbascum phlomoides*, which is hardly grazed by either livestock species.

Table 4: Result of the SAS mixed-linear-model analysis of the percentage of grazed phytomass differentiated into three plant functional types. Significant effects are shown in bold print.
Num df: degrees of freedom Numerator, Den df: degrees of freedom Denominator, p: level of significance.

Tab. 4: Ergebnis der Analyse gemischt linearer Modelle für den prozentualen Phytomasse-Entzug, differenziert nach unterschiedlichen funktionellen Gruppen. Signifikante Ergebnisse sind fett gedruckt. Num df: Freiheitsgrade des Numerators, Den df: Freiheitsgrade des Denominators, p: Signifikanzniveau.

effect	Num df	Den df	F Value	p
year	**1**	**12**	**7.98**	**0.0153**
animal	**2**	**12**	**13.36**	**0.0009**
year*animal	2	12	3.74	0.0545
plant functional type (PFT)	**2**	**24**	**16.01**	**<0.0001**
year*PFT	**2**	**17**	**8.10**	**0.0034**
animal*PFT	**4**	**24**	**7.13**	**0.0006**
animal*year*PFT	4	17	0.43	0.7876
vegetation type	**1**	**12**	**19.83**	**0.0008**
year*vegetation type	**1**	**12**	**4.77**	**0.0495**
animal*vegetation type	2	12	3.57	0.0609
animal*year*vegetation type	2	12	1.07	0.3725
vegetation type*PFT	**2**	**24**	**3.55**	**0.0447**
year*vegetation type*PFT	2	17	0.96	0.5605
animal*vegetation type*PFT	4	24	2.36	0.0823
animal*year*vegetation type*PFT	**4**	**17**	**4.24**	**0.0146**

Table 5: Mean percentages of grazed phytomass for every investigated category resulting from the mixed-linear-model analysis of the differentiated data-set shown in Table 4. The standard error is given in parentheses.
a,b,c: average values that are marked with different letters are significantly different within one row, A: *Armerio-Festucetum trachyphyllae typicum*, F: *Festuca duvalii*-subtype, PFT: plant functional type, g: graminoids, l: legumes, h: herbs (without l); differentiated data from Fig. 4.

Tab. 5: Mittlerer prozentualer Phytomasse-Entzug für alle untersuchten Unterkategorien. Die Ergebnisse resultieren aus der in Tab. 4 dargestellten Analyse gemischt linearer Modelle für den differenzierten Datensatz. Der Standardfehler ist in Klammern angegeben.
a,b,c: Mittelwerte, die mit unterschiedlichen Buchstaben markiert sind, unterscheiden sich innerhalb einer Reihe signifikant, A: *Armerio-Festucetum trachyphyllae typicum*, F: *Festuca duvalii*-subtype, PFT: funktionelle Pflanzengruppe, g: Graminoide, l: Leguminosen, h: Kräuter (ohne l); aufgeschlüsselte Daten der Fig. 4.

year	veg. type	PFT	sheep	donkeys	sheep + donkeys
2003	A	g	50.7 (10.1) **a**	50.2 (10.01) **a**	71.2 (6.6) **a**
2003	A	h	97.8 (4.7) **a**	93.3 (4.7) **a**	93.1 (4.7) **a**
2003	A	l	86.1 (6.6) **a**	84.2 (6.6) **a**	95.6 (6.6) **a**
2003	F	g	25.5 (10.1) **a**	66.3 (10.1) **b**	62.7 (10.1) **b**
2003	F	h	69.7 (6.7) **a**	43.8 (4.7) **b**	87.8 (4.7) **c**
2003	F	l	43.9 (6.6) **a**	81.1 (6.6) **b**	80.0 (6.6) **b**
2004	A	g	55.6 (7.8) **ab**	47.0 (7.8) **a**	74.2 (7.8) **b**
2004	A	h	72.6 (9.6) **a**	34.7 (9.6) **b**	75.3 (9.6) **a**
2004	A	l	80.8 (9.4) **a**	72.9 (9.4) **a**	77.9 (9.4) **a**
2004	F	g	54.8 (7.8) **a**	53.7 (7.8) **a**	75.5 (7.8) **a**
2004	F	h	75.1 (9.6) **a**	46.9 (9.6) **ab**	41.8 (9.6) **b**
2004	F	l	49.9 (9.4) **a**	63.4 (9.4) **ab**	83.8 (9.4) **b**

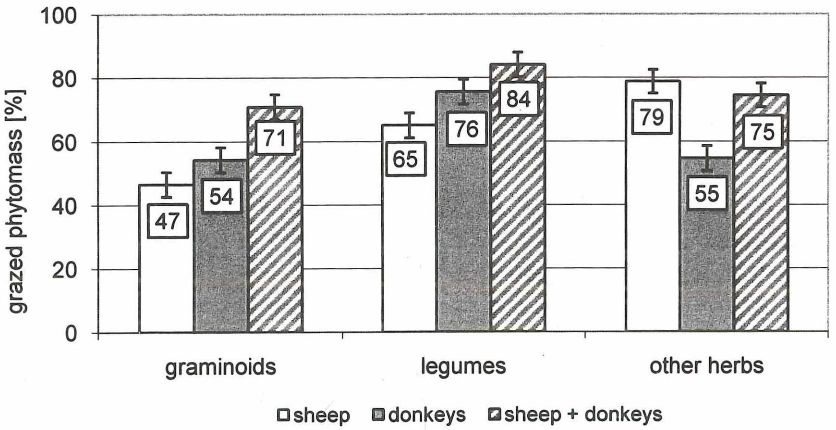

Fig. 5: Mean percentages of grazed phytomass for the three treatments resulting from the mixed-linear-model analysis of the differentiated data set. Error: Standard error.

Abb. 5: Mittlerer prozentualer Phytomasse-Entzug für die drei Weideregimes. Die Ergebnisse resultieren aus der Analyse gemischt linearer Modelle für den differenzierten Datensatz. Fehlerbalken: Standardfehler.

Table 6: Median of the grazing preferences (of both years and vegetation types) of sheep and donkeys for plant species with more than 3 records. 0: not or hardly grazed (0–5 % phytomass extraction), +: grazed (6–50 %), ++: intensively grazed (> 50 %), dot: no data. Red List species for Hesse are marked with R. K-C: *Koelerio-Corynephoretea* species, F-B = *Festuco-Brometea* species.

Tab. 6: Mediane der Fraßpräferenzen (über beide Jahre und Vegetationstypen) von Schafen und Eseln für Pflanzenarten, die auf mehr als 3 Flächen auftraten. 0: nicht oder kaum beweidet (0–5 % Phytomasse-Entzug), +: beweidet (6–50 % Phytomasse-Entzug), ++: intensiv beweidet (> 50%). Punkt: Keine Daten. Arten der Roten Liste Hessen sind mit R markiert. Arten der *Koelerio-Corynephoretea* mit K-C, Arten der Festuco-Brometea mit F-B.

			Sheep	Donkeys
		Graminoids		
K-C	R	Koeleria macrantha	++	++
K-C	R*	Festuca duvalii*/trachyphylla/ovina agg.	+	+
		Poa angustifolia	++	++
		Elymus repens	++	+
		Bromus tectorum	++	0
		Bromus hordeaceus	+	++
		Carex hirta	+	++
		Bromus inermis	+	.
		Cynodon dactylon	.	++
		Legumes		
K-C	R	Medicago minima	++	++
K-C		Trifolium arvense	++	++
K-C	R	Vicia lathyroides	++	.
		Medicago falcata + M. x varia	++	++
K-C		Trifolium campestre	++	+
F-B		Ononis repens	+	0
		Herbs (excl. legumes)		
K-C	R	Armeria maritima ssp. elongata	++	+
K-C	R	Silene conica	++	+
K-C		Rumex acetosella	++	+
K-C		Erodium cicutarium agg.	+	+
K-C		Petrorhagia prolifera	.	++
K-C		Echium vulgare	0	++
K-C		Arenaria serpyllifolia agg.	.	+
		Cerastium arvense	0	+
K-C		Potentilla argentea	0	0
		Conyza canadensis	++	++
		Chenopodium album agg.	++	++
		Berteroa incana	++	+
		Sisymbrium altissimum	+	+
		Saponaria officinalis	++	0
F-B		Centaurea stoebe	++	0
		Convolvulus arvensis	++	0
		Crepis capillaris	++	0
		Silene latifolia ssp. alba	++	0
		Silene vulgaris	++	.
		Rumex thyrsiflorus	++	.
		Geranium molle	++	+
		Achillea millefolium	.	++
		Asparagus officinalis	.	++
		Carduus nutans	.	+
		Verbascum phlomoides	0	0
		Psyllium arenarium	0	.
F-B		Euphorbia cyparissias	0	.
		Capsella bursa-pastoris	.	0
		Oenothera biennis s.l.	.	0
		Plantago lanceolata	.	0
		Polygonum aviculare agg.	.	0
K-C		Sedum acre	.	0

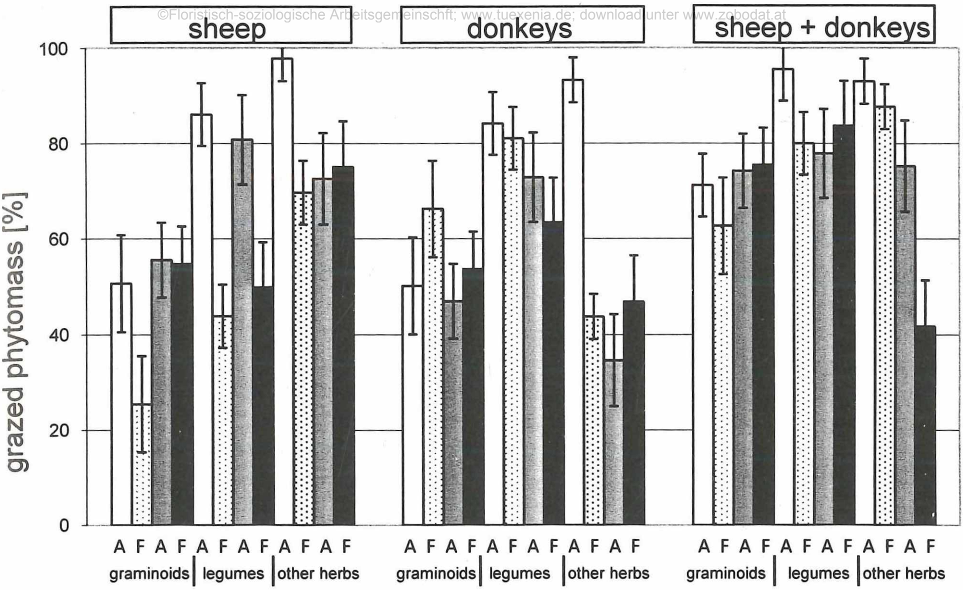

Fig. 4: Mean percentages of grazed phytomass for every investigated category. Error: Standard error (see Table 5: indication of significant differences).
A + white: *Armerio-Festucetum trachyphyllae typicum* 2003, F + dotted: *Festuca duvalii*-subtype 2003, A + grey: *Armerio-Festucetum trachyphyllae typicum*, 2004, F + black: *Festuca duvalii*-subtype 2004.

Abb. 4: Mittlerer prozentualer Phytomasse-Entzug für alle untersuchten Unterkategorien. Die Ergebnisse resultieren aus der Analyse gemischt linearer Modelle für den differenzierten Datensatz. Fehlerbalken: Standardfehler (s. Tab. 5: Angabe signifikanter Unterschiede).
A + weiß: *Armerio-Festucetum trachyphyllae typicum* 2003, F + punktiert: *Festuca duvalii*-subtype, 2003, A + grau: *Armerio-Festucetum trachyphyllae typicum* 2004, F + schwarz: *Festuca duvalii*-subtype, 2004.

5. Discussion

5.1. Phytomass extraction

Donkeys are supposed to need large phytomass intake because of their low nutrient extraction, and their dry-matter intake is high compared to that of other herbivores (AGANGA et al. 2000). The results show that with one-species grazing (either sheep or donkey) the mean extraction of phytomass was between 39 % and 65 %, but it depended strongly on the vegetation type. With successive two-species treatment, a maximum phytomass extraction was obtained. As a high phytomass extraction can cause the regression of grass-encroachment, influences the competition and creates gaps for the less competitive plant species, this can lead to a change in plant species composition. The change of species composition by a reduction of dominant grass species with multispecies grazing (ruminants and nonruminants) has been observed by LOUCOUGARAY et al. (2004) in coastal ecosystems in France.

5.2. Phytomass extraction of different PFTs

According to HÜLBER et al. (2005), "selective grazing occurs when the relative frequency of a food resource differs between the diet and the environment". In compliance with that definition, in our study sheep select for "other herbs" and "legumes", donkeys for "legumes". Usually livestock species prefer "legumes" to other plant species, probably due to their higher protein contents (STROH et al. 2002). Donkeys cannot store amino acids efficiently and therefore need a constant supply in their diet, which is provided by leguminous plant species (AGANGA et al. 2000). Sheep are also known as selective grazers which prefer plant species with higher protein contents (HAFEZ 1962, STROH et al. 2002). As is demonstrated in Table 5, the sheep's preference of herbs to legumes, as evidenced by the low phytomass extraction of legumes by sheep in the *Festuca duvalii*-subtype of the investigation area, can be explained by the high abundance of the legume species *Ononis repens* in that area; this plant is characterised by a high fibre content and thorns, so the animals prefer the leaves and reject the rough stem. The sheep's preference of leaves to stems has also been observed by O'REAGAIN (1993). This corresponds to the result that grasses – which usually have higher fibre contents – are least intensively grazed. Sheep, as a model species for ruminants, do not depend as heavily on roughage for their digestion as donkeys are known to do (JEROCH et al. 1999, AGANGA et al. 2000).

Equids are considered to be "true grazers" that feed predominantly on grasses (FAHNESTOCK & DETLING 1999, MENARD et al. 2002, LAMOOT 2004, LAMOOT et al. 2005b). Although within the percentage analysis donkeys do not differentiate between herbs and grasses, Fig. 1 demonstrates that graminoids form the main parts of their diet while herbs only contribute to a minor extent. Especially in the case of the *Armerio-Festucetum trachyphyllae typicum* in 2003, when relative phytomass extraction of herbs by donkeys was exceptionally high, this is due merely to an extremely low cover of herbal species. COSYNS et al. (2001) also observed a high graminoid biomass intake by donkeys and Konik horses for coastal dunes.

The investigation of the qualitative grazing preferences showed that only 50 % of the plant species were grazed by both animal species. In previous studies with cattle and horses as a model for ruminants and nonruminants, a qualitative dietary overlap of about 70 % was found (KRYSL et al. 1984, MCINNIS & VAVRA 1987). Thus the comparatively small value for sheep and donkeys suggests that the present two animal species can complement each other very well. Hence, phytomass extraction is often highest in the case of successive ruminant and nonruminant grazing. Another reason for the larger phytomass extraction in the case of the two-species treatment is the grazing of the donkeys' faeces-accumulation sites by sheep. In the case of equid grazing only, every year greater percentages of the paddock are used as faeces-accumulation sites with spreading ubiquitous nitrophytic plant species and ungrazed areas. This can be avoided by means of successive multispecies grazing (JEROCH et al. 1999, LOUCOUGARAY et al. 2004).

5.3. Differences between the years and vegetation types

The strong dependence on the year in case of the differentiated analyses of the PFTs is probably mainly due to the different plant species composition in the two investigated years. Because of the dry conditions in 2003, therophytes – often herbs – were almost absent. Together with the dependence on the vegetation type it was shown that dietary preferences depend not only on PFTs but also on detailed plant species composition and are thus strongly dependent on specific environmental conditions. Therefore it is very important to investigate different years with different environmental conditions (SÜSS et al. 2007).

6. Implications for the management of threatened sand vegetation

For purposes of nature protection, often a reduction of competitive grass species is necessary (KOOIJMAN & VAN DER MEULEN 1996, SÜSS et al. 2004). The results demonstrate that sheep as well as donkeys feed on these often clonal species and the maximum extraction of grasses can be achieved by successive two-species grazing. A 4-year study of the vegetation using 443 permanent plots à 25 m^2 (SÜSS & SCHWABE 2007) has demonstrated that the extraction of graminoids indeed caused a decrease in graminoid-cover in the following years and the percentage of bare ground increased. This was accompanied by an increase of gap pioneers such as *Potentilla argentea* and *Petrorhagia prolifera* (on donkey paddocks) and, e. g., *Centaurea stoebe* on sheep and donkey paddocks. Besides the reduction of grasses, an increase of herbs and therophytes as well as an increase of phytodiversity could also be achieved with all three grazing regimes for the investigated ecosystem (SÜSS & SCHWABE 2007). Combining these findings with the study of diet selection, it can be concluded that sheep as well as donkey grazing can be an adequate tool of nature conservation because the ruminants as well as the equids are able to reduce competitive grass species. Nevertheless, as shown above, donkey grazing should not be repeated too often due to the occurrence of faeces-accumulation sites. Transferring these findings to other low-productivity ecosystems, it can be concluded that due to the high phytomass extraction successive sheep and donkey grazing will be the most effective management method in the case of more ruderal and consolidated sites, because in these cases high phytomass extraction can have the strongest effects on plant species composition.

Problematic for sheep as well as for donkey grazing is the impact on endangered Red List species by grazing and trampling, if the grazing period starts too early. Hence care must be taken that grazing takes place after the fruiting period of these species (in our case Red List species of Hesse [BUTTLER et al. 1996] are: *Armeria maritima* ssp. *elongata*, *Festuca duvalii*, *Koeleria macrantha*, *Medicago minima*, *Silene conica*, *S. otites* and *Vicia lathyroides*).

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