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Sward structure and diet selection after sheep introduction on abandoned grassland in the Giant Mts, Czech Republic

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Abstract: The effect of rotational grazing on the sward structure of long-term abandoned grassland and the sheep diet selection were investigated in the Giant Mts (Krkonoše/Karkonosze). The aim of the study was to answer the following questions: (1) Does sheep grazing affect the sward structure of previously abandoned mountain grassland? (2) How does sheep diet selection develop within and among grazing seasons? (3) Which section of a pasture do sheep prefer to graze? Data was collected three times during each grazing season in spring, summer and in autumn in the years 2001, 2002 and 2003. Fifty 1 × 1 m plots were used where the plant species occurrence and damage of plants by grazing for all species were repeatedly recorded. 1) Nonsignificant changes in plant species occurrences were recorded in spite of obvious visual changes in sward structure due to grazing e.g. the retreat of tall dominant species characteristic of long-term unmanaged grasslands. 2) Seasonal as well as inter-annual changes in sheep diet selection were detected. In spring 2001, sheep grazed over a wide variety of plant species in low quantities. In subsequent springs, they preferred species favoured during previous autumns (*Veratrum album* subsp. *lobelianum*; *Ranunculus platanifolius*; *Senecio ovatus*) and changed the diet only as a result of the elimination of favoured plants. 3) Sheep preferred to graze at the highest elevated part of the pasture probably as a consequence of anti-predator behaviour not due to higher occurrence of favoured plant species or the presence of a drinking place or salt licks. Changes in the sward structure were mostly of a quantitative not qualitative character, thus the presence-absence data collection is not a suitable method for monitoring the effects of management restoration. The diet selection changed probably due to the animals' experience; sheep had no experience with montane species in spring 2001. The sheep were able to recognize favoured plant species after 6 months of wintering in lowland.

Key words: grassland degradation; grazing preferences and behaviour; restoration management; Krkonoše/Karkonosze

Introduction

The ability of herbivores to selectively graze better quality components of the sward or favoured plant species has been widely documented in many studies (Heady 1964; Coleman 1992; Dumont et al. 1995; Mayland & Shrewmaker 1999; Dumont et al. 2002; Garcia et al. 2003). In practice, various methods were used to study the diet selection and they can be generally divided into two broad types: 1) methods directly connected with animals such as the analysis of fecal and rumen contents (Homolka & Heroldová 1992; Heroldová 1996; Mellado et al. 2004), esophageal fistulation (Henley et al. 2001; Woji & Iji 1996) and direct observations of grazing animals (Dumont & Boissy 2000); or, alternatively, 2) methods based on vegetation such as the measurement of sward height (Correl et al. 2003; Barthram et al. 2005), biomass sampling of grazed plots and ungrazed control (Lepš et al. 1995) or direct estimation of grazing damage caused by bites upon individual plant species on the pasture (Bílek et al. 2000; Stroh et al. 2002).

Direct observation of grazing animals, biomass sampling and the estimation of grazing damage are the only methods enabling the precise determination of diet selection in species-rich swards composed of many plant species.

The advantages of grazing damage estimation are that it records the diet selection of the whole flock in the long term, not simply selected individuals during the short period of the day. The method can be practised in variable terrain where the visibility of grazers is restricted. Plant species can be easily classified according to selection by herbivores even in less accessible pastures in mountain areas. Knowledge of plant species selection or avoidance is extremely important if grazing is

Table 1. Mean cover of selected plant species before the establishment of the experiment in spring 2000. *Senecio* spp. = *S. ovatus* and *S. hercynicus*.

Species (Graminoids)	Cover [%]	Species (Other species)	Cover [%]	Species (Other species)	Cover [%]
Luzula luzuloides	12.7	*Hypericum maculatum*	12.6	*Epilobium angustifolium*	0.1
Holcus mollis	12.6	*Senecio* spp.	8.2	*Vaccinium myrtillus*	0.1
Calamagrostis villosa	7	*Silene vulgaris*	5.1	*Alchemilla* sp.	0.02
Deschampsia cespitosa	6.1	*Rumex arifolius*	4.1	*Epilobium alpestre*	0.02
Avenella flexuosa	4.5	*Geranium sylvaticum*	3.5	*Taraxacum* sp.	0.02
Agrostis capillaris	3.4	*Ranunculus platanifolius*	2.5	*Rubus idaeus*	0.01
Alopecurus pratensis	2.0	*Polygonatum verticillatum*	1.5	*Veronica chamaedrys*	0.01
Festuca rubra agg.	2.0	*Polygonum bistorta*	1.5	*Crepis conyzifolia*	0.0003
Juncus filiformis	0.6	*Galeopsis tetrahit*	1.2	*Myosotis nemorosa*	0.0002
Carex nigra	0.5	*Veratrum lobelianum*	0.7	*Chaerophyllum hirsutum*	0.0002
Poa trivialis	0.5	*Silene dioica*	0.5	*Maianthemum bifolium*	0.0002
Anthoxanthum sp.	0.04	*Stellaria nemorum*	0.5	*Ranunculus acris*	0.0002
		Trientalis europaea	0.4	*Solidago virgaurea*	0.0002
		Rumex alpinus	0.3	*Phyteuma spicatum*	0.0002
		Galium saxatile	0.3	*Campanula bohemica*	0.0002
		Gentiana asclepiadea	0.3	*Hieracium alpinum* agg.	0.0001
		Athyrium distentifolium	0.1	*Salix* sp. (juv.)	0.0001
Graminoids (total)	51.94			Other species (total)	45.6

applied as restorative management on degraded grasslands. It is also important when a risk of the spreading of avoided species or the extinction of highly preferred plant species exists (Krahulec et al. 2001; Matějková et al. 2003).

In this study, investigated sheep were transported from lowland to mountains and thus they had no experience with mountain plant species before the experiment started. Sheep grazing was introduced within the context of the re-establishment of grassland management aimed at the restoration of degraded, long-term abandoned mountain grasslands in the Krkonoše National Park. Regarding the fact that foraging was often studied in species-poor artificial swards, the re-establishment of regular management gave a unique opportunity to study changes in sward structure after the establishment of grazing together with the study of sheep diet selection and the animal's adaptability to new plant species present in the species-rich sward.

The aim of our study was to answer the following questions: 1) How does sheep grazing affect sward structure of degraded mountain grassland? 2) How does sheep diet selection develop within and among grazing seasons and how is it affected by the grazers' experience? 3) Which section of a paddock do sheep prefer to graze and is the preferred site connected with a higher occurrence of favoured plant species?

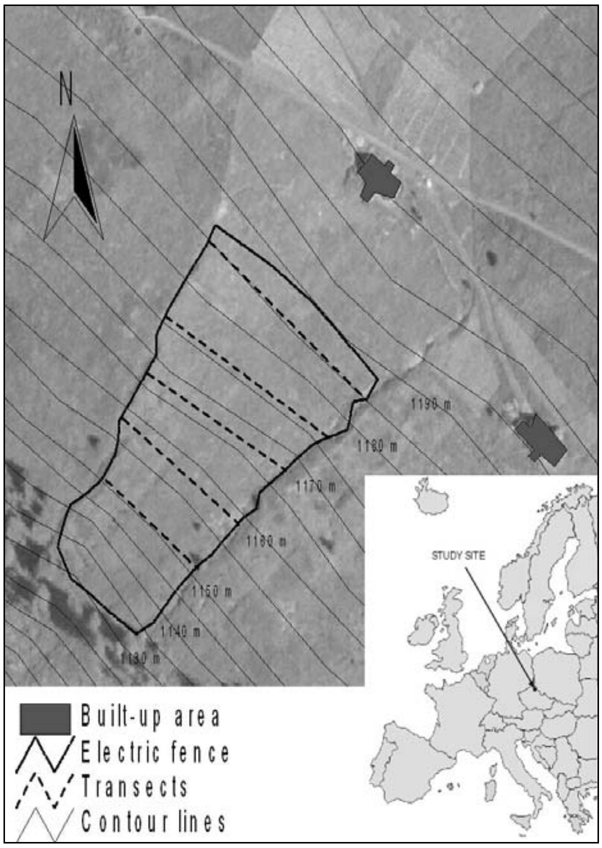

Fig. 1. Location of the investigated area in Europe and plan of the investigated paddock; electric fence limiting study area, transects where data was collected, contour lines in 5 m intervals and build-up area are marked. Orthophotomap was taken in 2002 thus managed area is clearly visible.

Material and methods

Study site

Klínové Boudy enclave (50°42′ N, 15°39′ E) lies in the eastern part of the Krkonoše National Park at an altitude of 1140–1280 m a. s. l. on a south-facing slope (Fig. 1). The mean annual temperature was between 3–4 ℃ and the mean annual precipitation was 1100 mm (Vrbatova bouda meteorological station). The bedrock is an acidic coarse-grain gneiss and mica-schist. The vegetation of the enclave was represented by the degradation phases of original *Nardus stricta* dominated grasslands (alliance *Nardion strictae* Br.-Bl. 1926).

Luzula luzuloides, Holcus mollis, Calamagrostis villosa and *Deschampsia cespitosa* were dominant graminoids; *Hy-*

pericum maculatum, Senecio ovatus, S. hercynicus and *Silene vulgaris* were dominant forbs before the establishment of grazing management (Table 1). *Senecio ovatus* and *S. hercynicus* were not distinguished, as the identification of defoliated stems later in the vegetation seasons was not possible.

Grazing management

Regular management of the summit area of the Giant Mts was ceased after the Second World War (Hejcman et al. 2006). Traditional management consisted of mowing once a year and cattle grazing in the autumn. Sheep grazing in the investigated area started in 2001. All observations were performed in an experimental paddock of 1 ha. This approach was used due to the extremely high variability of vegetation in the study site. The sward structure in other paddocks was completely different; that is why unmanaged control plots or comparisons with other paddocks were not possible to apply. Three grazing cycles (spring, summer and autumn) were applied in the experimental paddock during the run of the experiment. To maintain the same intensity of grazing in the paddock in all seasons, animals were moved away when 40–50% of available forage was grazed. Sheep were grazed rotationally in two surrounding paddocks when they were not in the experimental paddock. In spring, the experimental paddock was managed first, immediately when sheep started grazing in the study area.

In the first year of the experiment, twelve adult sheep were used. In the second year, twenty inexperienced and twelve experienced adults from the previous vegetation season were used. Twenty four experienced adults from one or two previous seasons were grazed in the last experimental season in 2003. A mobile electric fence was used to fence both experimental and other paddocks. Animals were kept without any shelter and supplementary feeding. Drinking water was available ad libitum from two water streams bordering the investigated paddock from the SE and NW. Sheep were introduced from lowland pasture therefore they had no experience of grazing mountain plant species before the experiment started. The flock was brought back into lowland each October for wintertime.

Data collection

Data was collected three times during each grazing season in June (spring grazing cycle), July (summer grazing cycle) and in August (autumn grazing cycle) in 2001, 2002 and 2003. At each recording, the data collection was performed after 3 days of grazing. Additionally, quantification of grazing damage was done before the sheep were moved away from the experimental paddock in autumn 2003. Permanent plots 1 × 1 m were used to record plant species occurrence and damage caused by grazing for all species. These 1m^2 plots were situated in five contour transects, each composed of 10 permanent plots, situated at a distance of 20 meters apart (50 monitoring plots in total; Fig. 1). To avoid problems with rare plant species, data was analysed only for the 16 most frequent species from 46 recorded. In investigated plots, species occurrence and presence of grazing damage of individual species were recorded in the form of qualitative data (yes/no). After an analysis of preliminary data from two vegetation seasons (Hejcman et al. 2004), grazing damage of plants was quantified before grazing cessation in autumn 2003. Grazing damage was estimated directly as a percentage of grazed aboveground biomass for each species in each plot. To estimate the extent of grazing damage precisely, we calibrated it for each plant species in neighbouring non-grazed vegetation outside the investigated paddock. This method was used earlier to classify the level of plant species selection on sand grassland communities managed by sheep grazing in southern Germany (Stroh et al. 2002). Nomenclature of plant species follows Kubát et al. (2002).

Data analysis

Multivariate diet selection data was analysed by constrained ordinations. Species frequency data was evaluated by both constrained and unconstrained ordinations. Constrained ordination with linear response (Redundancy analysis – RDA) in the CANOCO package (ter Braak & Šmilauer 2002) followed by Monte Carlo permutation test ($n = 999$) was used to evaluate trends in plant frequencies and diet selection. Constrained ordination with linear response was used because the environmental gradient was relatively short and years or seasons were coded as categorical explanatory variables. Unconstrained ordination was used to evaluate species frequency data. Principal component analysis (PCA) was used and samples' scores for four ordination axes from PCA analysis of species presence data explaining more than 78% of variability were treated as covariables in the RDA analyses of diet selection. Comparison of RDA analyses of diet selection with and without these covariables enabled the determination of changes in diet selection caused by the disappearance of particular species from a forage offer. To reveal the effect of altitude on grazing intensity, linear regression was used in the STATISTICA 6.0 program.

Results

The sward structure in the spring of 2001, before the establishment of experimental grazing, is shown in Table 1. *Luzula luzuloides, Holcus mollis, Calamagrostis villosa*, *Deschampsia cespitosa, Agrostis capillaris* and *Avenella flexuosa* were dominant graminoids. *Hypericum maculatum, Silene vulgaris, Rumex arifolius, Senecie ovatus, Geranium sylvaticum* and *Ranunculus platanifolius* were dominant forbs in the sward before the establishment of grazing. The species occurrence and grazing frequencies for the 16 most common species are shown in Figs 2 and 3. Grasses were the most often grazed species; in particular, *Agrostis capillaris* and *Holcus mollis* showed the highest proportion of grazed biomass and were thus the main components of sheep diet. Conversely, *Galium saxatile*, *Maianthemum bifolium* and *Trientalis europaea* were species never grazed during three experimental seasons.

Species frequencies

The year had a significant effect on the plant species' frequencies, with the exception of the spring data set, that displayed a nonsignificant trend only (Table 2). The percentage of variability explained by the effect of the year was 19.7, 29.4 and 29.8 in the spring, summer and autumn data sets, respectively. The spring data set was little affected by grazing in the particular season, so the major changes in plant frequencies were caused by year to year variation and by the grazing effects on the development of the plant community. *Agrostis capillaris*, *Hypericum maculatum*, *Ranunculus platanifolius, Rumex arifolius* and *Senecio* spp. occurred in more than 50% of the plots in the spring of 2001; the

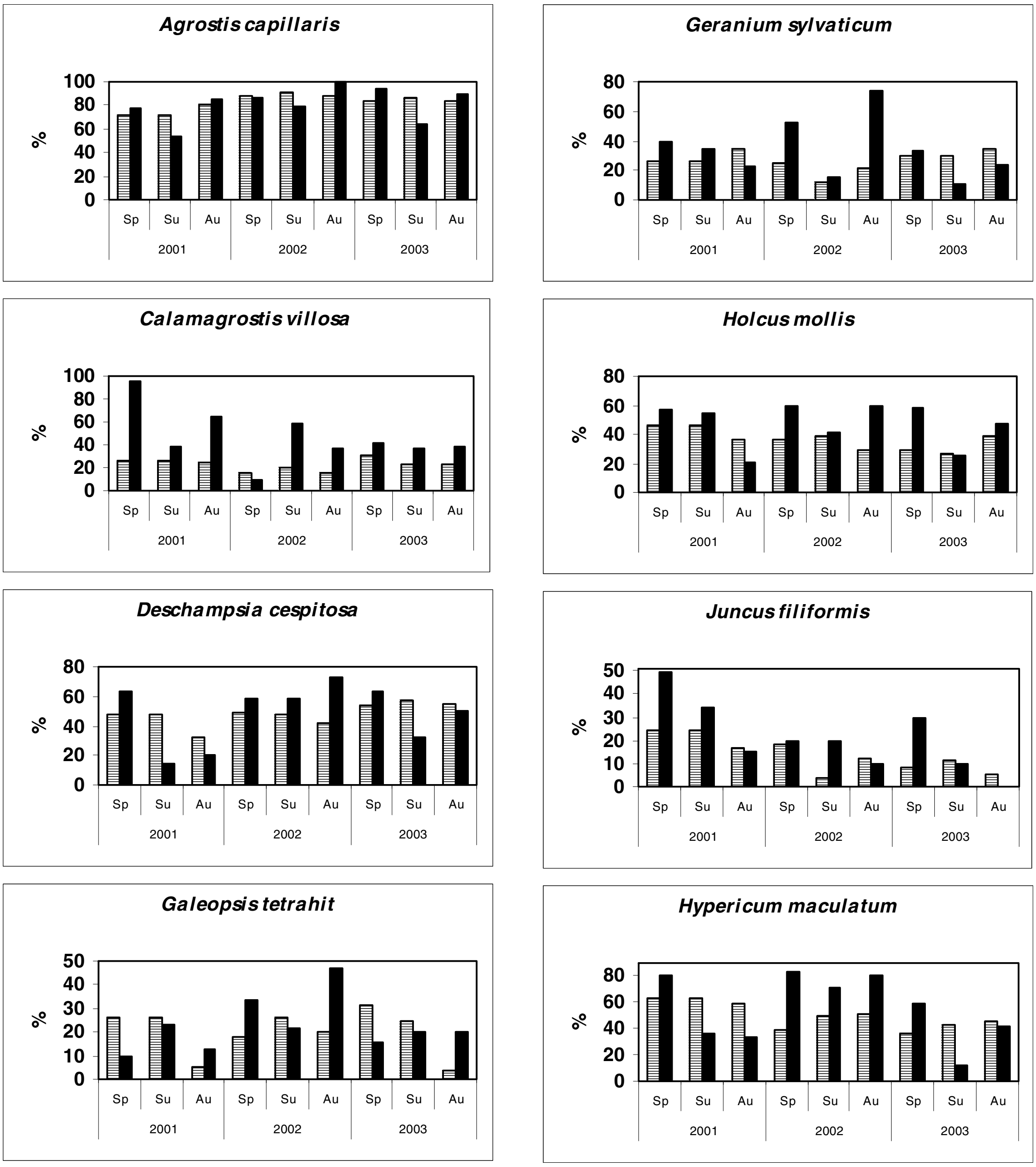

Fig. 2. Occurrence of species as a percentage from all investigated plots (strip columns) and presence of grazing as a percentage from all plots where the species was recorded (black columns). Sp – spring, Su – summer, Au – autumn; 2001, 2002 and 2003 – years of the investigation.

Table 2. RDA analyses of interannual changes in spring, summer and autumn species occurrences (analyses A1 – A3) and PCA analysis of all species occurrences data (analysis A4). PlotID = plot identification; Exp. var. = explanatory variables; % expl. var. = variability explained by first (all) axis; P – value = probability value obtained by Monte Carlo permutation test. Analysis A4 was indirect gradient analysis and sample scores for four ordination axes were used as covariables in RDA analyses of grazing presence/absence data in Tables 3 and 4.

Analysis	Exp. var.	Covariable	% expl. var.	P – value
A1: spring data	Year	PlotID	19.7	0.064
A2: summer data	Year	PlotID	29.4	0.004
A3: autumn data	Year	PlotID	29.8	0.004
A4: indirectPCA			30.9 (78.1)	

distribution of these species was thus relatively homogeneous in the investigated area. *Calamagrostis villosa* and *Luzula luzuloides*, which were also species with relatively high cover, showed conspicuous patchiness. The retreat of *Holcus mollis*, *Hypericum maculatum, Juncus filiformis*, *Ranunculus platanifolius* and *Senecio* spp. in spring data after two years of grazing was recorded. *Agrostis capillaris*, on the other hand, increased its fre-

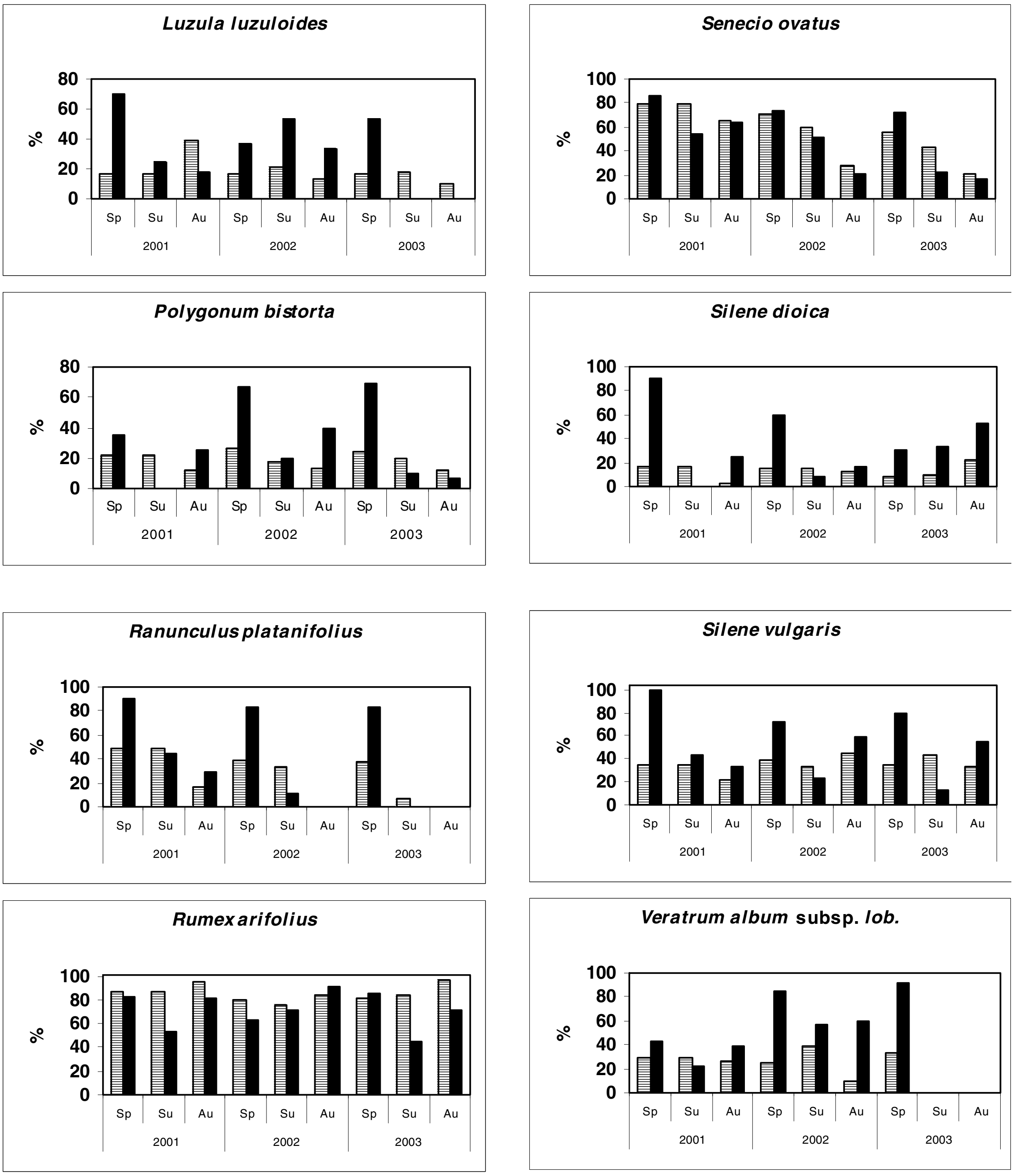

Fig. 3. Occurrence of species as a percentage from all investigated plots (strip columns) and presence of grazing as a percentage from all plots where the species was recorded (black columns). Sp – spring, Su – summer, Au – autumn; 2001, 2002 and 2003 – years of the investigation.

quency in the three-year-grazed sward (Figs 2, 3).

Effect of season on diet selection
Interannual differences were recorded in diet selection – effect of the year was significant and explained 36.3, 35.4 and 37.1% of diet selection variability in the spring, summer and autumn data sets respectively (Table 3, analyses A1a – A3a). To show how much of this variability was caused by species frequencies, analyses A1b – A3b were performed. None of these three analyses was significant after removing the majority of species presence effect from analyses of diet selection. Sheep changed their diet selection at least partly because plant species composition of available forage varied each year.

Effect of year on diet selection
Significant changes in sheep diet selection were revealed in each year of the experimentation. Effect of the time within season explained 49.7, 35.8 and 55.8% of diet selection variability in 2001, 2002 and 2003, respectively (Table 4, analyses A1a – A3a). To demonstrate how much of this variability was caused by plant species, occurrence analyses A1b – A3b were performed. Analysis of the data set from the year 2001 (A1b) was significant for the first axis as well as for all constrained ordination

Table 3. RDA analyses of grazing presence/absence data – an effect of year on spring, summer and autumn diet selection. Sample scores for four ordination axes obtained from analysis A4 in Table 2 were used as covariables in analyses A1b – A3b. PlotID = plot identification; Y1, Y2 and Y3 – years 2001, 2002 and 2003 coded in the form of dummy variables. Exp. var. = explanatory variables; % expl. var. = variability explained by first (all) constrained axis, P – value = probability value obtained by Monte Carlo permutation test for the first (all) constrained ordination axes.

Analysis	Exp. Var.	Covariable	% expl. var.	P – value
A1a: spring data	Y1, Y2, Y3	PlotID	29.4 (36.3)	0.016 (0.026)
A2a: summer data	Y1, Y2, Y3	PlotID	22.5 (35.4)	0.048 (0.016)
A3a: autumn data	Y1, Y2, Y3	PlotID	25.3 (37.1)	0.02 (0.01)
A1b: spring data	Y1, Y2, Y3	PlotID, Score	30.6 (44.0)	0.29 (0.202)
A2b: summer data	Y1, Y2, Y3	PlotID, Score	31.1 (39.9)	0.238 (0.296)
A3b: autumn data	Y1, Y2, Y3	PlotID, Score	40.8 (53.8)	0.086 (0.054)

Table 4. RDA analyses of grazing presence/absence data – changes in diet selection in three investigated seasons evaluated separately. Sample scores for four ordination axes obtained from analysis A4 in Table 2 were used as covariables in analyses A1b – A3b. PlotID = plot identification; Sp, Su and Au – spring, summer and autumn coded in the form of dummy variables. Exp. var. = explanatory variables; % expl. var. = variability explained by first (all) constrained axis, P – value = probability value obtained by Monte Carlo permutation test for the first (all) constrained ordination axes.

Analysis	Exp. Var.	Covariable	% expl. var.	P – value
A1a: 2001	Sp, Su, Au	PlotID	42.3 (49.7)	0.004 (0.004)
A2a: 2002	Sp, Su, Au	PlotID	24.6 (35.8)	0.006 (0.006)
A3a: 2003	Sp, Su, Au	PlotID	50 (55.8)	0.004 (0.01)
A1b: 2001	Sp, Su, Au	PlotID, Score	70.6 (70.6)	0.016 (0.038)
A2b:2002	Sp, Su, Au	PlotID, Score	37.6 (58.1)	0.114 (0.022)
A3b: 2003	Sp, Su, Au	PlotID, Score	20.6 (32.4)	0.54 (0.43)

Table 5. RDA analyses of grazing presence/absence data (analyses A1 and A2) and species occurrences data (analysis A3) taken in autumn 2003. Effect of altitude on diet selection and plant species distribution was evaluated. Sample scores for four ordination axes from PCA analysis (A4) were used as covariables in analysis A2. Exp. var. = explanatory variable; % expl. var. = variability explained by first (all) constrained axis, P – value = probability value obtained by Monte Carlo permutation test for the first constrained ordination axe.

Analysis	Exp. var.	Covariable	% expl. var.	P – value
A1: graz. pref.	Altitude		38.5	0.002
A2: graz. pref.	Altitude	Score	8.9	0.008
A3: occurence	Altitude		6.9	0.02
A4: indirect PCA			22.7 (62.1)	

axes. Sheep changed their diet selection within the first experimental season, although the biomass of species grazed in spring was still available later in the vegetation season. The sheep tested a wide scale of species when they came to the pasture but the selection frequency of particular species was low. In the spring of 2001, grazing frequencies were high also for species little grazed in next seasons; namely for *Calamagrostis villosa*, *Juncus filiformis* and *Luzula luzuloides* (Figs 2, 3). The analysis of the data set from the year 2002 (A2b) was significant only for all constrained axes. There were changes in diet selection during the year 2002, but without any remarkable differentiation of spring preferences from other parts of the year. The analysis of the data set from the year 2003 (A3b) was significant neither for first, nor for all constrained ordination axes. No changes in diet selection were detected after removing the majority of species occurrence effect. The sheep changed their diet selection only due to the elimination of favoured plant species from the forage on offer in 2003. *Ranunculus platanifolius*, *Senecio* spp. and *Veratrum album* subsp. *lobelianum* were plant species preferred by the sheep in the spring of 2002 and 2003. In 2003, *Veratrum* was eliminated from the forage offer quickly after the start of the grazing season, thus *Veratrum* was not recorded in the summer and autumn data (Fig. 3). The sheep grazed leaves and stems causing a total disappearance of *Veratrum* from the available forage. A similar grazing interest was recorded for *Ranunculus platanifolius* as well. There was a substantial difference in changes in grazing preference between the first and the third experimental season.

Effect of altitude on sheep diet selection

The plant species composition of the investigated paddock was affected by the altitude – the effect of altitude was significant and explained 6.9% of species data variability (analysis A3 in Table 5). *Deschampsia cespitosa, Calamagrostis villosa, Rumex arifolius* and *Silene dioica* were more abundant in the upper part of the investigated paddock; *Agrostis capillaris*, *Geranium sylvatium, Hypericum maculatum, Juncus filiformis* and

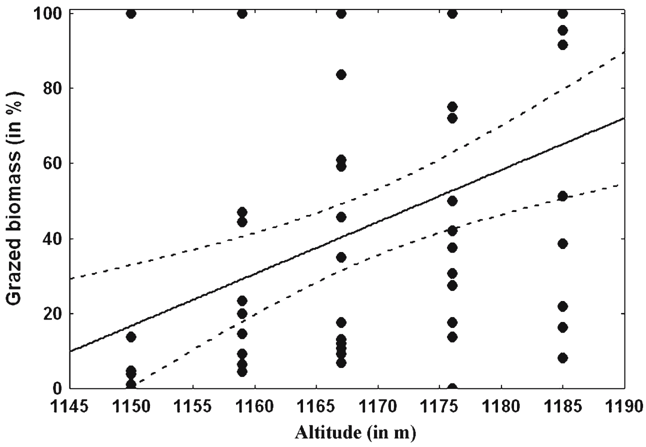

Fig. 4. Percentage of grazed biomass in monitoring plots as a function of altitude in autumn 2003. Sheep preferred to graze the upper part of the paddock. Intermittent lines indicate a 95% confidence interval.

Senecio spp. were spread without any significant relationship to altitude; *Silene vulgaris*, *Luzula luzuloides*, *Polygonum bistorta*, *Galeopsis tetrahit* and *Holcus mollis* were more frequent in the bottom part of the investigated pasture.

The altitude explained 38.5% of sheep diet selection and its effect was significant. The analysis A2 in Table 5 showed that diet selection was also affected by altitude after removing the effect of species frequencies. The sheep preferred to graze the upper part of the investigated paddock and this was not caused by a more frequent occurrence of favoured plant species. Although there was a high variability in grazing intensity in the paddock, the effect of altitude on the percentage of grazed biomass in the monitoring plots was significant in the final stages of the last experimental season (Fig. 4; $R^2 = 0.21$; $F = 14.6$; $P < 0.001$).

Discussion

The sheep grazed a wide scale of plant species during the three investigated grazing seasons. *Galium saxatile*, *Maianthemum bifolium* and *Trientalis europaea* were never amongst the grazed species. All these short forbs were often located under a higher grass and herb layer and were avoided probably due to their bad visibility in the sward and probably on account of their unpalatability, particularly in the case of *Maianthemum bifolium.* This is in accordance with Dumont et al. (2000) who showed that spatial distribution of sward components can be decisive for the grazing of different plants and their organs.

Species frequencies

The effect of the year on spring species frequencies was not significant although substantial changes in the sward structure due to grazing were recorded. Quantitative, not qualitative changes in the sward structure occurred: some species changed their biomass production or cover due to grazing, but none of the plant species disappeared from the sward and none of the new plant species were discovered on the pasture. To analyse changes in vegetation, the collection of quantitative data, cover or biomass production of all present species, is much more suitable. *Hypericum maculatum* decreased in the investigated paddock. In the spring of 2003, subtle plants were recorded as a result of two previous seasons of grazing. Frequent defoliation restricted the dominance of this forb in previously long-term unmanaged sward and this was consistent with other studies (Krahulec et al. 2001; Hejcman et al. 2005). *Juncus filiformis* decreased probably due to sheep grazing and trampling. Regular grazing of this species was relatively surprising; *Juncus* species generally belong to unpalatable plants grazed in periods of forage shortage only. *Ranunculus platanifolius* decreased on account of defoliation caused by intensive grazing of this species. This species evidently does not cope with frequent defoliation. That is probably why *Ranunculus platanifolius* was relatively rare in regularly managed grasslands in the Giant Mts *Senecio* spp. , a tall and typical dominant forb of mountain clearings or unmanaged grasslands (Hejcman et al. 2005), was a highly palatable species for sheep and it was sensitive to defoliation. Frequent grazing of this species was recorded by horses and cows in other localities as well (Hejcman, unpublished data). *Agrostis capillaris*, a typical pasture plant in the Czech mountains, increased on account of grazing. *Agrostis capillaris* obviously possesses a high defoliation tolerance enabling its spreading under grazing (Pavlů et al. 2003). Changes in vegetation structure are clearly visible from spring species occurrences in Figures 2 and 3. The decrease of undesirable plant species, characteristic for long term unmanaged sward, indicated that sheep grazing was a promising alternative management of degraded meadows in the Giant Mts.

Diet selection

Changes in diet selection were the most interesting fact. Dissimilarity in diet selection amongst three grazing seasons was probably caused by the lack of experience of sheep grazing on montane species in 2001. The sheep sampled a wide range of species present on the pasture in 2001. In the spring of 2001, the frequent grazing of *Calamagrostis villosa, Juncus filiformis, Luzula luzuloides* and *Silene dioica* contrasted with their omission in the following two seasons. The testing of unknown plant species was a possible reason why the highest frequencies of little damaged plants were recorded the spring of 2001. When meeting new species, the sheep ate a small quantity and awaited a health response. The fact that unknown plant species are generally eaten in small quantities is in accordance with Provenza (1995). If post-ingestive malaise does not occur, herbivores start to eat new species or new food in higher quantity (Villalba & Provenza 1999; Provenza et al. 2003; Papachristou et al. 2005).

Although a part of the flock had no experience of montane species in 2002, the sheep were able to adapt their diet selection relatively quickly. Herbivores learned to select plant species through trial and error as well as via social models from experienced animals. This was in accordance with previous studies (Provenza & Balph 1988; Provenza 1991). Herbivores were able to learn to select species quickly within several days and were able to recognize favoured species after six months when they were in a shed or on a lowland pasture during wintertime. This was clearly visible from the diet selection of *Veratrum.* This species started to be favoured in the autumn of 2001. In the following spring, sheep with experience from the previous grazing season immediately started to graze this species. The same situation occurred between autumn 2002 and spring 2003. In the spring of 2003, this species was preferentially grazed by all sheep until its total and rapid disappearance from the forage offer (Fig. 3). According to Schaffner et al. (2001) and Kleijn & Steinger (2002), *Veratrum* was a local dominant avoided by large herbivores able to restrict plants of higher forage quality. The revealed preferential grazing of *Veratrum* by sheep was in accordance with Krahulec et al. (2001). This species was probably of lower toxicity for sheep than for cattle. Mixed grazing of sheep with large herbivores is thus probably a useful tool for *Veratrum* control in mountain pastures. *Veratrum* was grazed so quickly, that its generative reproduction was impossible in this experiment. The same changes in diet selection were recorded for *Ranunculus platanifolius* as well. The sheep preferred *Ranunculus* in the spring of 2002 and 2003 until its total disappearance. *Senecio* spp. was regularly grazed and especially leaves and inflorescences were selected first. The remaining dry stems were only recorded in the autumn. *Agrostis capillaris, Geranium sylvaticum, Holcus mollis, Rumex arifolius* and *Silene vulgaris* were grazed relatively uniformly without any detectable trends. They were able to re-grow after defoliation thus the quality of their biomass was rather stable and still palatable. *Hypericum maculatum* was regularly selected in each season with a peak in 2002. In 2003, a decrease in grazing was probably due to changes in plant dispersion from considerable patchiness to a more regular pattern. *Hypericum* was thus probably less visible for sheep on the pasture in 2003. The visibility and character of plant dispersion are decisive factors for preference or avoidance of particular species on the pasture (Heady 1964; Dumont et al. 2002; Rook et al. 2004). According to Krahulec et al. (2001), *Deschampsia cespitosa* was unpalatable and little grazed by sheep. In this experiment, *Deschampsia cespitosa* was regularly grazed similarly to an experiment with cows performed by Matějková et al. (2003). A different sward structure and grazing technique were probably responsible for different results. The palatability of particular species must be related to the investigated sward. The extrapolation of conclusions without a description of grazing management may be faulty. *Silene dioica*, particularly its stems, was often grazed in 2001. The change in the growth strategy of this species was recorded under grazing: the majority of plants had the characteristic of rosettes with leaves close to the soil surface in the third grazing season. In each season, *Galeopsis tetrahit* was regularly grazed, particularly in summer and autumn, despite its roughness. The occurrence of this species was not affected by three seasons of grazing.

Effect of altitude on sheep diet selection

No effect of plant distribution on the intensity of grazing in relation to the altitude was revealed. Frequent sheep grazing in the upper part of the investigated paddock was probably caused by anti-predator behaviour in relation to the open landscape and by their good view of the surrounding terrain. The same preference of other sheep breeds for the highest part of the pasture was also described by Bílek & Žáková (1997), Bílek et al. (2000) and by Mládek (personal communication). To maintain a uniform pasture in slopping terrain in a protected area, a paddock constructed with a super elevation as low as possible is probably a better solution than attracting animals by supplementary feeding, a drinking place, or a shelter in the bottom parts of the pasture. According to the experience of farmers, attraction of sheep by supplementary feeding resulted in excessive sward disturbances and the creation of pathways without vegetation. Excessive disturbances contradicted the conservation status of the national park.

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References

Barthram G.T., Duff E.I., Elston D.A., Griffiths J.H., Common T.G. & Marriott C.A. 2005. Frequency distributions of sward height under sheep grazing. Grass Forage Sci. **60:** 4–16.

Bílek M. & Žáková I. 1997. Ethological observations of the regeneration sheep grazing in the Krkonoše National Park, p.127. In: ISAE '97, Proceedings of the 31st International Congress of ISAE, Prague.

Bílek M., Žáková I. & Bendová P. 2000. Grazing behaviour of ewes in the course of restoration of species diversity of mountain meadows in a protected area. Acta zootechnica, VÚŽV Uhříněves, **1:** 18–23.

Coleman S.W. 1992. Plant – animal interface. J. Prod. Agric. **5:** 7–13.

Correl O., Isselstein J. & Pavlů V. 2003. Studying spatial and temporal dynamics of sward structure at low stocking densities: the use of an extended rising-plate-meter method. Grass Forage Sci. **58:** 450–454.

Dumont B. & Boissy A. 2000. Grazing behaviour of sheep in a situation of conflict between feeding and social motivations. Behav. Process. **49:** 131–138.

Dumont B., Carrere P. & D'Hour P. 2002. Foraging in patchy grasslands: diet selection by sheep and cattle is affected by the abundance and spatial distribution of preferred species. Anim. Res. **51:** 367–381.

Dumont B., Maillard J.F. & Petit M. 2000. The effect of the spatial distribution of plant species within the sward on the searching success of sheep when foraging. Grass Forage Sci. **55:** 138–145.

Dumont B., Petit M. & D'Hour P. 1995. Choice of sheep and cattle between vegetative and reproductive cocksfoot patches. Appl. Anim. Behav. Sci. **43:** 1–15.

Garcia F., Carrere P., Soussana F. & Baumont R. 2003. How do severity and frequency of grazing affect sward characteristics and the choices of sheep during the grazing season? Grass Forage Sci. **58:** 138–150.

Heady H.F. 1964. Palatability of herbage and animal preference. J. Range Manage. **17:** 76–82.

Hejcman M., Auf D. & Gaisler J. 2005. Year-round cattle grazing as an alternative management of hay meadows in the Giant Mts (Krkonoše, Karkonosze), the Czech Republic. Ekológia, Bratislava, **24:** 419–429.

Hejcman M., Pavlů V., Hejcmanová P., Gaisler J., Hakl J. & Rauch O. 2006. Farmer decision making and its effect on the subalpine grassland succession in the Giant Mountains, Czech Republic. Acta Soc. Bot. Pol. **75:** 165–174.

Hejcman M., Žáková I., Bílek M. & Stránská M. 2004. Reestablishment of grassland management in the Klínové boudy locality – Sheep diet selection and sward structure under defoliation. Opera Corcontica **41:** 552–559.

Henley S.R., Smith D.G. & Raats J.G. 2001. Evaluation of 3 techniques for determining diet composition. J. Range Manage. **54:** 582–588.

Heroldová M. 1996. Dietary overlap of three ungulate species in the Palava Biosphere Reserve. For. Ecol. Manage. **88:** 139–142.

Homolka M. & Heroldová M. 1992. Similarity of results of stomach and faecal contents analyses in studies of the ungulate diet. Folia Zool. **41:** 193–208.

Kleijn D. & Steinger T. 2002. Contrasting effects of grazing and hay cutting on the spatial and genetic population structure of *Veratrum album*, an unpalatable, long-lived, clonal plant species. J. Ecol. **90:** 360–370.

Krahulec F., Skálová H., Herben T., Hadincová V., Wildová R. & Pecháčková S. 2001. Vegetation changes following sheep grazing in abandoned mountain meadows. Appl. Veg. Sci. **4:** 97–102.

Kubát K., Hrouda L., Chrtek J.jun., Kaplan Z., Kirschner J. & Štěpánek J . (eds) 2002. Klíč ke květeně České republiky. Academia, Praha.

Lepš J., Michálek J., Kulíšek P. & Uhlík P. 1995. Use of paired plots and multivariate analysis for the determination of goat grazing preference. J. Veg. Sci. **6:** 37–42.

Matějkova I., van Diggelen R. & Prach K. 2003. An attempt to restore Czech species-rich mountain grassland through grazing. Appl. Veg. Sci. **6:** 161–168.

Mayland H.F. & Shrewmaker G.E. 1999. Plant attributes that affect livestock selection and intake, pp. 28–35. In: Proceedings Grazing Behavior of Livestock and Wildlife. Idaho Forest, Wildlife and Range Exp. Sta. Bull. No. 70, University of Idaho, Moscow.

Mellado M., Rodriquez A., Villarreal J.A. & Lopez R. 2004. Height to withers and abdominal circumference effects on diets of grazing goats. Appl. Anim. Behav. Sci. **88:** 263–274.

Papachristou T.G., Dziba L.E. & Provenza F.D. 2005. Foraging ecology of goats and sheep on wooded rangelands. Small Rumin. Res. **59:** 141–156.

Pavlů V., Hejcman M., Pavlů L. & Gaisler J. 2003. Effect of rotational and continuous grazing on vegetation of an upland grassland in the Jizerske hory Mts, Czech Republic. Folia Geobot. **38:** 21–34.

Provenza F.D. 1991. Behavior and nutrition are complementary endeavors, pp. 157–169. In: Proceedings 2nd Grazing Livestock Nutrition Conference, Agric. Expt. Sta. MP-133. Oklahoma State Univ., Stillwater.

Provenza F.D. 1995. Postingestive feedback as an elementary determinant of food selection and intake in ruminants. J. Range Manage. **48:** 2–17.

Provenza F.D. & Balph D.F. 1988. Development of dietary choice in livestock on rangelands and its implications for management. J. Anim. Sci. **66:** 2356–2368.

Provenza F.D., Villalba J.J., Dziba L.E., Atwood S.B. & Banner R.E. 2003. Linking herbivore experience, varied diets and plant biochemical diversity. Small Rumin. Res. **49:** 257–274.

Rook A.J., Dumont B., Isselstein J., Osoro K., WallisDeVries M.F., Parente G. & Mills J. 2004. Matching type of livestock to desired biodiversity outcomes in pastures – a review. Biol. Conserv. **119:** 137–150.

Schaffner U., Kleijn D., Brown V. & Müller-Schärer H. 2001. *Veratrum album* in montane grasslands: a model system for implementing biological control in land management practices for high biodiversity habitats. Biocontrol/News and Information **22:** 19–28.

Stroh M., Storm Ch., Zehm A. & Schwabe A. 2002. Restorative grazing as a tool for directed succession with diaspore inoculation: the model of sand ecosystems. Phytocoenol. **32:** 595–625.

Ter Braak C.J.F. & Šmilauer P. 2002. CANOCO Reference manual and CanoDraw for Windows user's guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, New York, USA.

Villalba J.J. & Provenza F. 1999. Effects of food structure and nutritional quality and animal nutritional state on intake behaviour and food preferences of sheep. Appl. Anim. Behav. Sci. **63:** 145–163.

Woji A.Y. & Iji P.A. 1996. Oesophageal fistulation of West African Dwarf sheep and goats for nutritional studies. Small Rumin. Res. **21:** 133–137.

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