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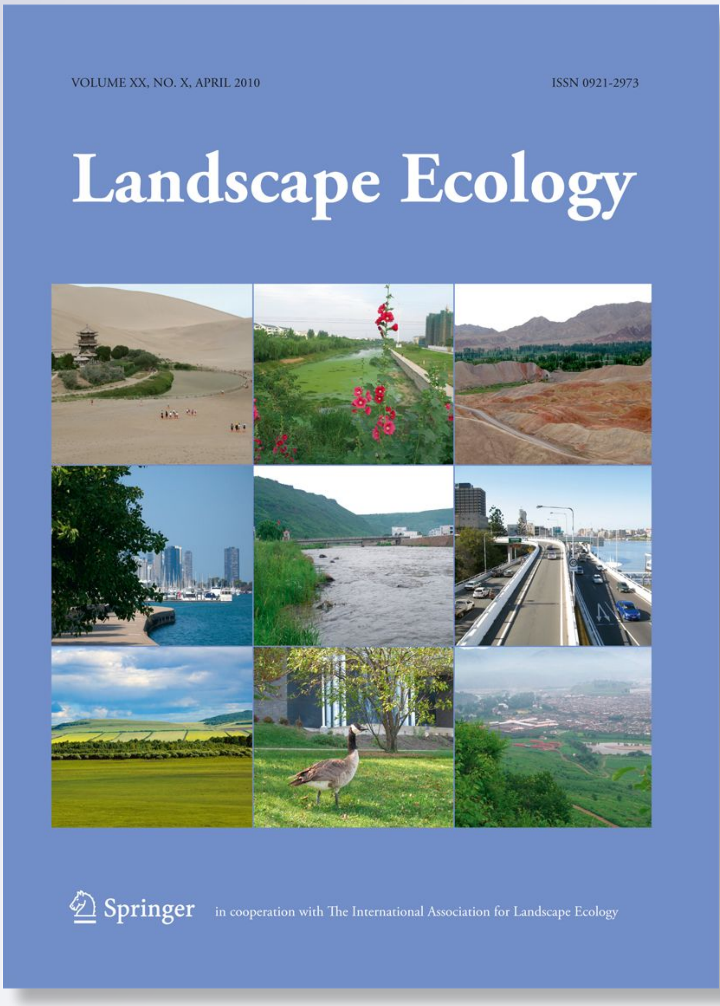

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RESEARCH ARTICLE

The effect of plant spatial pattern within a patch on foraging selectivity of grazing sheep

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Abstract Plant spatial pattern has been considered as one of the most important factors influencing forage selection of herbivores in natural grasslands. Previous work has emphasized the effects of spatial distribution patterns of food resource at the scale of whole plant communities. Our objective was to explore whether changes in spatial patterns of food within a patchy site affected forage selection of sheep within and among patches. We conducted a manipulative experiment using three native plant species of different palatability and abundance to artificially create three different quality patches in each treatment. We compared the effects of aggregated and randomly dispersed patterns, within high, medium, and low quality patches respectively, on sheep forage selection. Effects of plant spatial patterns within a patch on sheep forage selection of the patch itself strongly depended on the patch quality. For high quality patches, random dispersion of food resources significantly decreased sheep consumption of the palatable plant within the patch. This effect was reversed in low quality patches, and was not significant in medium quality patches. Changes in plant spatial patterns within high quality patches greatly influenced sheep forage selection of other patches. However, changes in plant spatial patterns within medium or low quality patches significantly influenced foraging responses of sheep only for high quality patches. We therefore conclude that high quality resource sites are the most influential and susceptible foraging areas. Our results highlight the importance of high quality resource sites when considering grazing grassland conservation and management.

Keywords Diet selection · Foraging decision · Plant spatial distribution · Spatial scale

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Introduction

The food resources of rangeland herbivores are typically patchily distributed, and often form a mosaic of patches of different forage quality and quantity (Kotliar and Wiens 1990). Herbivores have evolved a range of foraging strategies in response to this spatial heterogeneity in the distribution of food resources (Senft et al. 1987; Boone 2007; Fryxell et al. 2008; Morellet et al. 2011). Optimal foraging theory predicts that diet selection by large generalist herbivores is greatly influenced by trade-offs between the benefits of ingesting a given diet component and the costs of searching and selecting for it (Charnov 1976; Stephens and Krebs 1986). When traveling and exploiting cost represent a significant energy cost, the pattern of food resource distribution is likely to be one of the most important factors influencing forage selection of herbivores in natural grasslands (WallisDeVries 1996; Parsons and Dumont 2003; Hewitson et al. 2005; Wang et al. 2010a, b).

The spatial pattern of food resources can change across spatial scales. Resource-containing patches may be aggregated or dispersed in space, while at a smaller scale, there may be aggregation or dispersion in the distribution of food resources within patches. Most previous work has emphasized effects of overall spatial distribution pattern of patchy food resource throughout the grazing area (Edwards et al. 1994; Dumont et al. 2002). Evidence suggests that a clumped distribution of preferred plant species favors its consumption by herbivore and greatly improves foraging efficiency (Clarke et al. 1995; Dumont et al. 2000). Conversely, a random dispersion of unpalatable plant patches greatly reduces herbivore intake of the palatable species (Wang et al. 2010a). However, little is known whether spatial distribution pattern within patches has a significant influence on forage selection of herbivores.

Selective foraging by herbivores has been described as a nested hierarchy of decisions taken at different spatial scales from plant individual within a patch, and patches, to plant communities and landscape types (Senft et al. 1987; Bailey et al. 1996). Selection can occur at each scale level and may accumulate across scale levels (Ward and Saltz 1994; Frair et al. 2005; Harata et al. 2006; Kohler et al. 2006). Foraging decisions at broader spatial scales can constrain choices at lower levels. For example, the patch type greatly influences individual tree browsing by wild herbivores (Baraza et al. 2006; Miller et al. 2009). Furthermore, consequences of lower-scale decisions may be used to develop expectations of alternatives at higher scales (Bailey et al. 1996; Newman 2007). For instance, selectivity by sheep among patches is greatly reduced when plant neighborhood relationships within patches are intricate (Wang et al. 2010b). The location of a plant and its association with the surrounding vegetation strongly determine herbivore foraging decision on the food patch choice (Bergman et al. 2005). Therefore, at a smaller scale, plant spatial pattern within patches may have large impacts on herbivore forage selection. Understanding this effect will bring us a closer step to explaining foraging behavior, and this will be useful in managing grazing in grasslands.

Here, our aim was to explore whether changes in spatial pattern of plants within a patchy site (i.e. plant spatial micro-pattern) affected forage selection of sheep at the larger patch scale. Specifically, we experimentally addressed the following questions about sheep foraging: (1) how do plant spatial patterns within different quality patches affect consumption of preferred species and the overall food intake in each patch? And (2) does patch quality play a part in explaining the effects of plant micro-patterns on forage selection?

Materials and methods

Experimental animals and plant species

The experiment was conducted at the Grassland Ecological Research Station of Northeast Normal University, Jilin Province, P. R. China (44°40′–44°44′N and 123°44′–123°47′E). Twelve 2-year-old male Northeast Fine-wool sheep (body weight 31.1 ± 0.75 kg mean ± SE), which were bred in northeast China, were used in this experiment.

We chose three native plant species which formed the main dietary components of sheep in the meadow steppe. All three species have the C_3 photosynthetic pathway. *Medicago sativa* is a legume with high protein content, *Phragmites australis* is a perennial grass with intermediate nutrient content, and *Leymus chinensis* is a dominant, perennial grass with low protein and high fiber contents. Their relative preference by sheep was determined in preliminary tests and the preference index (expressed as percentages, dividing intake of each food by the total intake of all three types of food) for *M. sativa*, *P. australis* and *L. chinensis* was 0.73, 0.27 and 0.01, respectively. Plant materials were harvested from the field in late July, air-dried, and crushed up as hays in pieces of about 10 cm in length.

Experimental treatments and design

Four food presentation treatments with different plant micro-patterns of different quality patches were created (Table 1; Fig. 1). There were three patches (high,

Table 1 Experimental design of four different plant spatial micro-pattern treatments

Treatments	Plant spatial micro-patterns		
	Within Hp	Within Mp	Within Lp
A (aggregated micro-patterns)	Aggregated	Aggregated	Aggregated
D-H (dispersed micro-pattern within Hp)	Dispersed	Aggregated	Aggregated
D-M (dispersed micro-pattern within Mp)	Aggregated	Dispersed	Aggregated
D-L (dispersed micro-pattern within Lp)	Aggregated	Aggregated	Dispersed

Hp high quality patch, *Mp* medium quality patch, *Lp* low quality patch

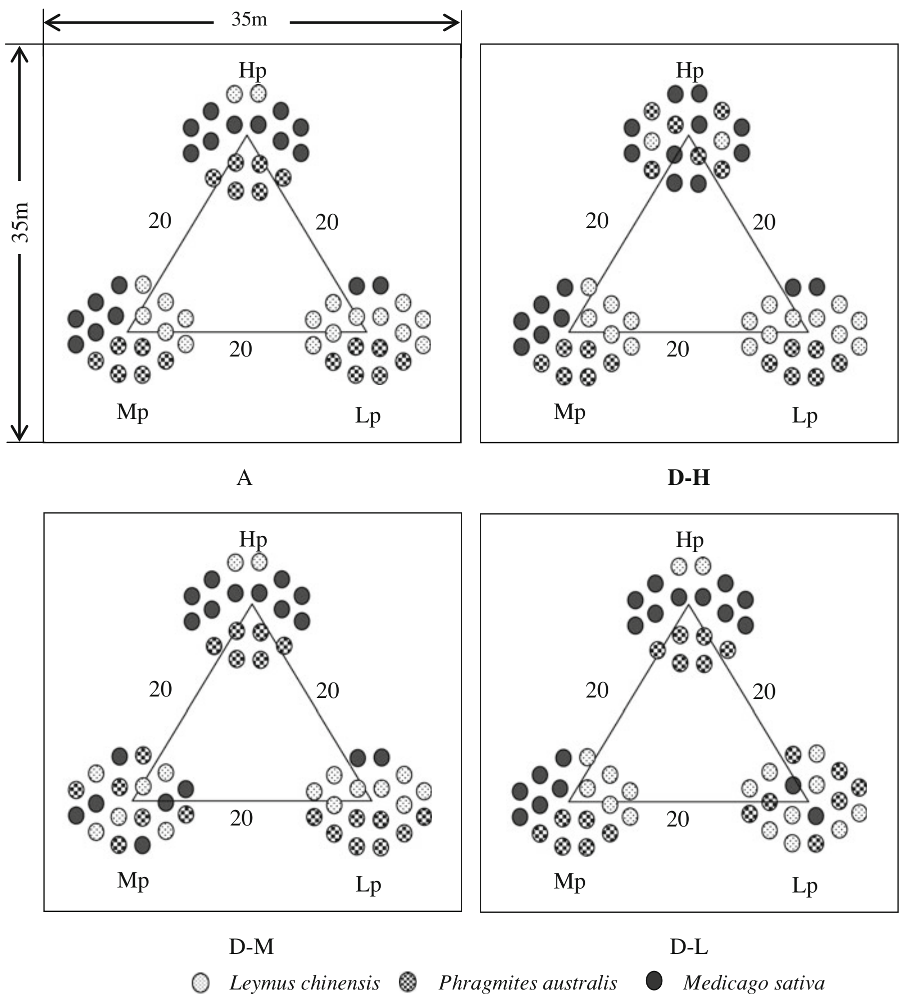

Fig. 1 Diagram of four food presentation treatments showing different plant spatial micro-patterns. *Hp* high quality patch, *Mp* medium quality patch, *Lp* low quality patch. **a** A: each plant species within each patch distributed aggregately, **b** D-H: plants within high quality patch dispersed, and within the other two patches kept aggregated, **c** D-M: plants within medium quality patch dispersed, **d** D-L: plants within low quality patch dispersed (three species were indicated by *black*, *striped* and *dotted filled circles*)

medium, and low quality patches, respectively) of the same size and shape, placed on each vertex in a triangle shape in each treatment plot. The distance between any two patches was 20 m. Each patch was 8 m in diameter and consisted of 18 troughs (30 cm in diameter, 15 cm high) equally spaced. The distance between centers of two adjacent troughs within each patch was 1.5–2 m. There was enough space for sheep to go back and forth between troughs. Plants previously harvested were distributed evenly over 54 troughs with 18 troughs per species. For each species, 1,200 g of plants was evenly divided to fill 18 troughs (see Fig. 1). There were 10 troughs of *M. sativa*, 6 troughs of *P. australis* and two troughs of *L. chinensis* in the high quality patch. For each medium quality patch, each plant species was equally distributed among 6 troughs. For low quality patches, there were 2 troughs of *M. sativa*, 6 of *P. australis* and 10 of *L. chinensis*, respectively. Troughs of different species within the three patches were distributed to create four plant spatial micro-patterns (see in Fig. 1). In the first micro-pattern, troughs of the same plant species were aggregated within each patch (treatment A). In the second micro-pattern, all the 18 troughs within high quality patch were dispersed randomly, and troughs of the same plant within medium quality patch and low quality patch were kept aggregated (treatment D-H). In the third micro-pattern, the spatial distribution of three plants within medium quality patch was dispersed randomly, and each of the three species within high quality patch and low quality patch were distributed aggregated (treatment D-M). For the fourth micro-pattern, plants distribution within low quality patch was random and each species within the other two patches were aggregated (treatment D-L). The 12 sheep were randomly divided into four groups of three sheep. These groups were allocated to the four food presentation treatments in a 4 × 4 Latin Square Design. Each treatment was repeated four times.

Field preparation and experimental procedure

Experiments were conducted in July–August 2008. Four 35 m × 35 m experimental fields were fenced and all vegetation was killed using herbicide before the experiment. Sheep were trained daily for 15 days to walk in the plots in groups and foraged from troughs to get accustomed to consuming the plants in troughs before the start of the experiment. There was a container full of fresh water in the middle of the patches during each trial.

The four plant spatial micro-pattern treatments were randomly arranged within the four plots with a group of three sheep for each plot. Experiment started from 5:00 to 6:00 am, and the fasted sheep were released from holding pens into the experimental field, allowed to feed for 1 h, and then removed back to holding pens. One hour was long enough for adequate response but short enough to avoid the complete removal of preferred food from all patches. The four groups of three sheep were tested only once a day. During each trial, the positions of the three patches were exchanged randomly precluding the effects of spatial memory on diet selection between trials. There were three observers standing along each plot side to record the feeding behavior of each sheep during experiment. Sequence of visits to different patches and the duration of each visit were recorded. A visit started when sheep approached a patch and lowered its head into a trough, and ended when it moved away from the patch. After feeding, the remaining plant materials in troughs were emptied into plastic bags assorted by plant species and patches and weighed. Food intake was then calculated.

Data analysis

Computed behavioral variables included: consumption of the preferred plant in each patch, total food intake and visiting time in each patch, sheep foraging selectivity between patches. We compared these behavioral variables of each patch in treatment A with that in treatment D-H, D-M, D-L respectively. The overall selectivity, as indicated by the difference between the composition of the diet and that of the available plants (Laca and Demment 1996), was examined. The overall selectivity index (OSI) was determined by the following equation:

$$\mathrm{OSI} = \frac{\sum_{i=1}^{n} (q_i - p_i)^2}{\max\limits_{1<i<n} \left\{ 1 - 2q_i + \sum_{i=1}^{n} q_i^2 \right\}}$$

where p_i is the proportions of patch options consumed, q_i is the proportions of patch options offered, and n is number of patches offered. OSI = 0 when the same proportions of each patch offered are consumed (i.e. completely unselective), and OSI = 1 when only one patch is consumed (i.e. completely selective).

The group of three sheep was the unit of replication. Behavioral data of individual sheep were averaged for each group. We analyzed effects of spatial micro-pattern treatments on the consumption of preferred plant species, the total food intake of all plant species, visiting time within high, medium and low quality patch respectively, and OSI between patches. All the statistical analyses were performed using SAS 6.12 statistical package (SAS Institute Inc. 1989). Assumptions of normality and heteroscedasticity were tested prior to analyses. All the above variables were analyzed using the General Linear Model procedure with the design being a Latin square. Whole plot independent variables were period, group of sheep, spatial micro-pattern treatment, and period × group of sheep × spatial micro-pattern treatment as the whole plot error term. Significance level was set at $P \leq 0.05$.

Results

Sheep consumption of the preferred plant species

Sheep consumption of preferred plant species (*M. sativa*) in high quality patches was significantly lower when plant spatial micro-pattern within high quality patch changed from aggregated to randomly dispersed. Meanwhile, intake of *M. sativa* in other two patches (medium and low quality patches) increased significantly ($P < 0.05$; Fig. 2a). However, compared with that in treatment A, sheep consumed more *M. sativa* at high quality patches in treatment D-M where plant spatial micro-pattern within medium quality patches was changed from aggregated to dispersed randomly ($P < 0.05$; Fig. 2b). And there was no significant difference in sheep consumption of the preferred plant species at medium quality patches and low quality patches between treatment A and D-M ($P > 0.05$; Fig. 2b). In treatment D-L, as plant spatial micro-pattern within low quality patches became dispersed, sheep consumed much more *M. sativa* in low quality patches, and significantly lower *M. sativa* at high quality patches compared with that in treatment A ($P < 0.05$; Fig. 2c).

The overall intake of sheep at each patch

Plant spatial micro-patterns significantly affected sheep's overall intake in each patch (Fig. 3). When plant micro-pattern within each patch was aggregated (treatment A), sheep exhibited high selectivity for high quality patches. The overall intakes of high, medium and low quality patches were 240.50, 187.30, and 101.40 g, respectively ($P < 0.01$). However, the overall intake in high quality patches significantly declined to 189.37 g when plant spatial pattern within high quality patches changed from aggregated to dispersed, and sheep's overall intake in medium quality patches significantly increased to 243.11 g ($P < 0.05$), and no obvious difference of overall intake in low quality patches (Fig. 3a). There was a greater intake in high quality patches in treatment D-M where the plant spatial micro-pattern within medium quality patches was dispersed randomly ($P < 0.01$), but this random pattern did not exert a significant influence on the food intake in medium quality patches and low quality patches (Fig. 3b). In treatment D-L where the micro-pattern within low quality patches was dispersed, sheep's overall intake significantly increased in low quality patches ($P < 0.01$) and decreased in high quality patches ($P < 0.01$; Fig. 3c).

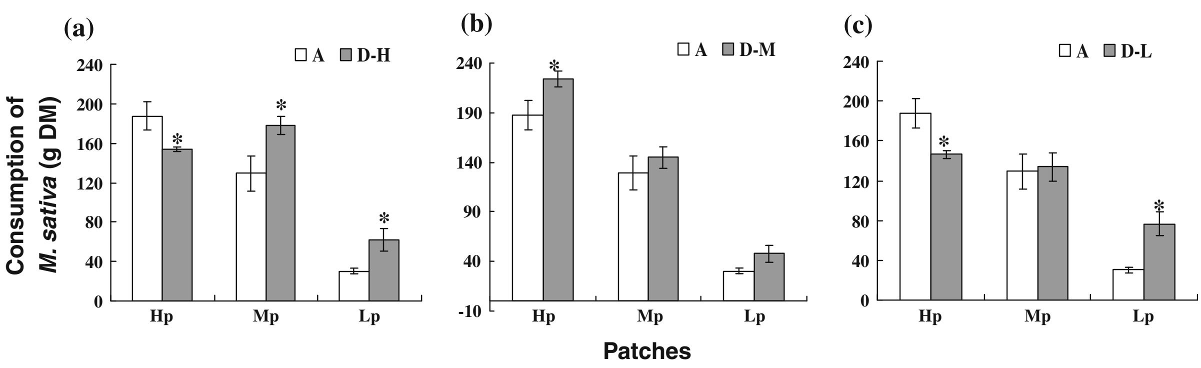

Fig. 2 Sheep consumption of preferred plant as affected by plant spatial micro-pattern treatments. *Hp* high quality patch, *Mp* medium quality patch, *Lp* low quality patch. **a**, **b**, **c** Comparing the consumption of preferred plant in each patch between treatment A and treatment D-H, D-M, D-L respectively. Values are means (±SE, n = 12) of all sheep. Values with *asterisk* are significantly different ($P < 0.05$)

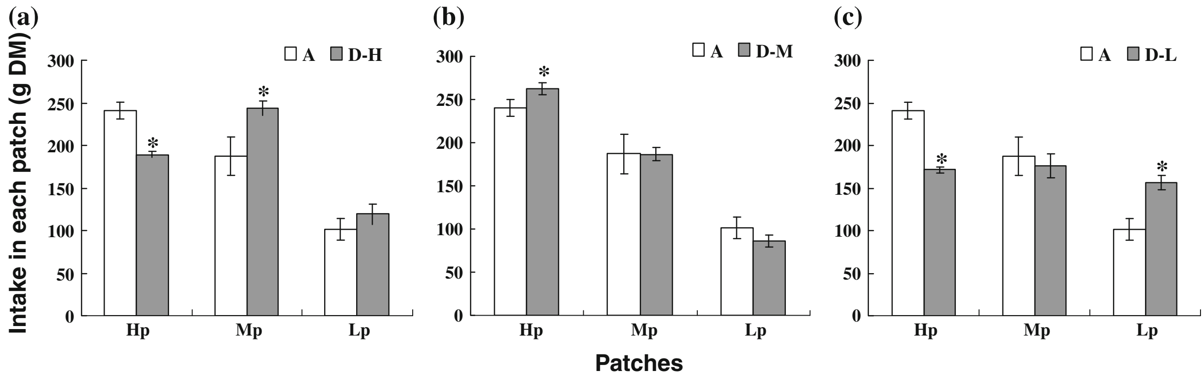

Fig. 3 Sheep overall consumption of each patch as affected by plant micro-pattern treatments. *Hp* high quality patch, *Mp* medium quality patch, *Lp* low quality patch. **a**, **b**, **c** Comparing the overall intake in each patch between treatment A and treatment D-H, D-M, D-L respectively. Values are means (±SE, n = 12) of all sheep. Values with *asterisk* are significantly different ($P < 0.05$)

OSI between patches

Plant spatial micro-pattern within patch significantly affected the between-patch OSI (Fig. 4). In the aggregated-distribution treatment (A), the OSI was relatively high. When plants were randomly distributed within high quality patches, but kept aggregated within the other two patches (treatment D-H), the OSI significantly declined compared with that in treatment A ($P < 0.05$). However, when the dispersed micro-pattern of plants occurred in medium quality patches (treatment D-M), OSI was significantly higher than treatment A ($P < 0.05$). But in treatment D-L, where there was a dispersed micro-pattern of plants in low quality patches, between-patch OSI was much lower than treatment A ($P < 0.05$).

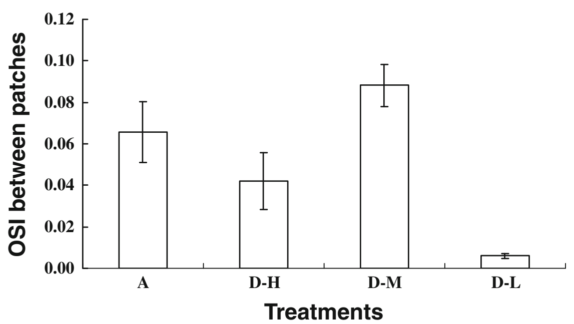

Fig. 4 Sheep forging selectivity between patches (OSI) as affected by plant micro-pattern treatments. OSI is significantly higher in treatment D-M than that in treatment A, but significantly lower in treatments D-H and D-L than that in treatment A ($P < 0.05$)

Visiting time in each patch

Sheep spent significantly less time in high quality patches when the micro-pattern within high quality patches turned from aggregated to dispersed (treatment D-H) ($P < 0.01$; Fig. 5a), and visiting time in medium and low quality patches were significantly higher. There was no significant difference in visit time between treatment A and D-M (Fig. 5b). Sheep spent significantly more time in low quality patches with less time staying in high quality patches in treatment D-L compared with that in treatment A ($P < 0.01$; Fig. 5c).

Discussion

For the first time, our study provided strong experimental evidence that plant spatial micro-pattern affected herbivore foraging selectivity at larger spatial scales. Changes in plant spatial distribution within a patch altered the internal structure of the patch, and caused a variation in the contrast between patches (Kotliar and Wiens 1990). It can thereby impact herbivore forage selection at both within- and between-patch scales. Our results demonstrated that plant spatial pattern within high quality patches significantly affected sheep forage selectivity in all patches. Meanwhile, plant micro-patterns within both medium and low quality patches greatly influenced sheep foraging selectivity in high quality patches. Therefore, the high quality food sites were the most

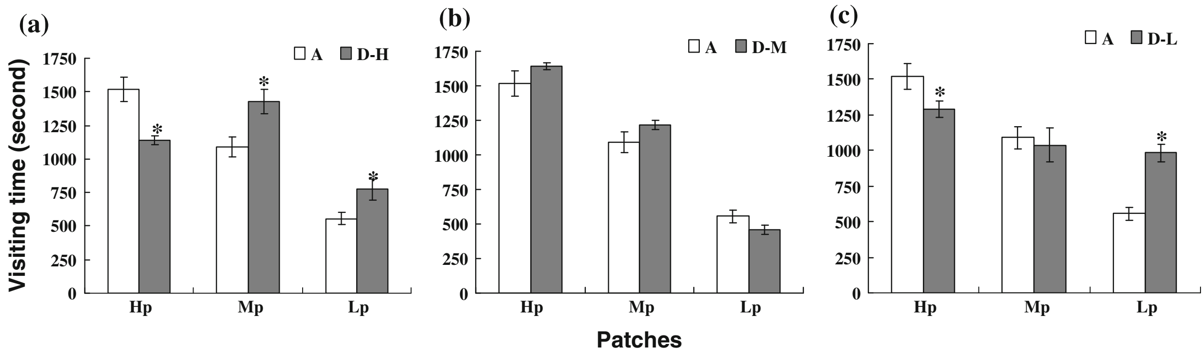

Fig. 5 Visiting time of sheep for three patches across micro-pattern treatments. *Hp* high quality patch, *Mp* medium quality patch, *Lp* low quality patch. **a**, **b**, **c** Visiting time to each patch in treatments D-H, D-M, D-L compared with treatment A respectively. Values are means (±SE, n = 12) of all sheep. Values with *asterisk* are significantly different ($P < 0.05$)

crucial area for sheep in response to the variations of plant spatial micro-pattern in grasslands.

It has been reported that sheep can make foraging decisions at finer spatial scales, and can discriminate among different plant species that are finely intermixed (Edwards et al. 1994; Wang et al. 2010c, 2011). In addition, responses of animals to a spatial scale may be modified by processes at other spatial scales (Newman 2007; Miller et al. 2009). In our study, consumption of the preferred species and overall intake in a patch were influenced by the change in sheep selectivity between and within patches resulting from the altered plant spatial micro-patterns. Plant micro-patterns within patches significantly affected sheep foraging judgment for patches as a whole. Outcomes of consumption of a patch depended on two foraging decisions: the probability of it being visited and how long the animals would stay and explore it once visited. Sheep often randomly visited each patch when they were not familiar with external characteristics of the patches (e.g. density, biomass or quality). Upon encountering a patch, they may make quick quality assessment and concentrate on preferred food patches utilizing spatial memory (Benhamou 1994; Edwards et al. 1996; Dumont and Petit 1998).

Our study found that sheep can accurately estimate the whole quality of each patch and thereby efficiently distributed their foraging to the most profitable patch when all plant species followed an aggregated distribution in all patches. They spent the most time and ingested a large amount of the preferred plant in high quality patches in treatment A. The result of the OSI also showed that sheep exhibited obvious selectivity between patches in treatment A (Fig. 4). Herbivores can adopt an area-concentrated foraging strategy to obtain foraging success when all food resources are aggregated (Benhamou 1992; Ward and Saltz 1994; Fortin 2003). An aggregated-distribution pattern probably reduced the cost of searching for palatable food, enhanced animal foraging efficiency, and made it easier for animals to use spatial memory to concentrate foraging in the profitable foraging area (Benhamou 1994; Dumont and Petit 1998; Laca 1998).

However, when plant spatial distribution changed from aggregated to dispersed within patches, foraging selectivity of sheep between patches significantly changed (Fig. 4). Spatial pattern within patches significantly affected sheep's foraging judgments for different quality patches. In treatment D-H, where plants within high quality patches followed a dispersed micro-pattern, between-patch OSI significantly declined compared to treatment A. Sheep reduced the time exploiting in high quality patches and meanwhile extended the time in medium and low quality patches. Both the amount of preferred plant and the overall intake significantly decreased in high quality patches, and increased in medium and low quality patches. It was evident that the dispersed distribution of plants greatly limited sheep ability to discriminate and estimate the patch quality. As previous studies demonstrated, the cost of foraging increased and foraging success for the preferred plant decreased in the dispersed distribution compared to aggregated distribution (WallisDeVries 1996; Dumont et al. 2002). Therefore, exploiting efforts of sheep shifted from high quality patches where it was costly for them to get the preferred plant to lower quality patches where the aggregated plant micro-patterns were easy to search and ingest their preferred food. In addition, the forage selection of a patch by herbivores depended largely on the estimates of the preferred food within the patch. Thus, overall intake decreased in high quality patches but increased in medium and low quality patches when micro-pattern within high quality patches followed a dispersed distribution. These results indicate that minor variation in plant distribution in high quality patchy sites could cause intense effects on foraging selectivity of sheep not only in the high quality patch itself, but also in other patches in the foraging area.

Results from this study further showed that effects of plant micro-pattern were significantly different in different quality of patches. Contrary to the pattern treatment of high quality patches (treatment D-H), sheep consumption for the preferred plant and overall intake significantly increased compared to treatment A when plants within low quality patch changed to a dispersed pattern (treatment D-L). Since the abundance of the preferred plant in low quality patch was lowest, the encounter rate with the palatable plant by herbivores may be greater in the dispersed than the aggregated patterns (Dumont et al. 2002). This would affect sheep foraging judgments for this patch, thereby increasing their staying and exploring time. Our results also showed that sheep extended the time staying in low quality patches when plants were randomly distributed in treatment D-L. Consequently, there was an increase in sheep intake in low quality patches, but a decrease in sheep foraging selectivity of both the preferred plant and the overall food intake in high quality patches because of their concentration on forage in low quality patches. Furthermore, in treatment D-M, we found that there was no significant difference in the consumption of the preferred plant and the overall intake in medium quality patches when plant distribution pattern in medium quality patches changed from aggregated to dispersed. However, the dispersed spatial pattern within both medium quality patches and low quality patches greatly affected foraging selectivity of sheep in high quality patches. We therefore concluded that effects of plant spatial pattern on sheep foraging greatly depended on abundance of preferred species, and that high quality patch sites were the most susceptible foraging areas in grazed grasslands.

Conclusions

Sheep can make judgments and foraging decisions at within- and between-patch scales according to different plant spatial patterns within different quality patches. When the plant micro-pattern changed from aggregated to dispersed in any grassland site, sheep foraging selectivity in high quality patches was consequently changed. Moreover, when changes in plant distribution occurred in high quality patches, there was an extensive effect on the foraging selectivity of sheep in every grassland site. Therefore, high quality sites were the most susceptible and functional foraging area. We highlight the importance of high quality sites when considering grassland conservation and management since regulating for high quality forage sites may extensively affect the whole grassland.

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