



Original article

Diet selection variation of a large herbivore in a feeding experiment with increasing species numbers and different plant functional group combinations

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ARTICLE INFO

Article history:

Received 1 October 2010

Accepted 14 February 2011

Available online 10 March 2011

Keywords:

Diet preference

Foraging selectivity

Foraging strategy

Plant species richness

Sheep

ABSTRACT

The grazing of domestic herbivores affects the biodiversity of rangeland. Knowledge on the feedback of changed plant diversity on diet selection by domestic herbivores is poor even though it is at the core of the effects of herbivores on biodiversity of rangeland. We investigated the influence of increasing species numbers and different plant functional group combinations on the dynamics of diet preference and foraging selectivity by sheep. Sheep were given 16 consecutive meals at each sequential level of plant species richness. Three combinations of species, selected for functional types, were presented to sheep. The results showed that sheep did not usually maintain stable diet preference patterns for the 16 consecutive meals of the plant species combinations offered. The magnitude of meal to meal variation in the preference index for each species increased significantly with plant species richness. There was no obvious effect of post-ingestive learning on the meal variation in diet preference. The magnitude of sheep foraging selectivity within each meal significantly reduced with plant species richness. These results indicated that, when plant diversity was high, the diet selection pattern of herbivore may be more beneficial to maintaining high plant diversity. Thus, there may be a weak positive feedback between plant species richness and herbivore foraging. We suggested that increasing plant diversity, especially for plant functional group diversity, can reduce herbivore selectivity and promote more uniform use of different plant species in rangeland.

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1. Introduction

Consideration of biodiversity is now important in rangeland management (Tilman et al., 1997; Hector et al., 1999; Chapin et al., 2000; Hooper et al., 2005). Grazing by large herbivores has been recognized for a long time as the major influence on the plant species richness and composition of plant communities (McNaughton et al., 1989; Collins et al., 1998; Knapp et al., 1999). Large grazing herbivores may affect plant diversity through many mechanisms including seed dispersal, urine and dung deposition and selective foraging (Olf and Ritchie, 1998). Foraging behavior of herbivores has the most direct influence on the diversity and dynamics of plant communities (Hodgson and Illius, 1996). There are many studies assessing the impact of herbivores grazing on plant diversity (Collins et al., 1998; Frank, 2005; Bakker et al., 2006). However, the foraging response of large herbivores to altered plant diversity receives little attention. The relationship between plant diversity and herbivore foraging is interactive, dynamic, and may involve feedback loops. We cannot

separate effects of herbivores on plant diversity from the effects of plant diversity on herbivore foraging in grazing ecosystems. Thus, pre-grazing level of plant species richness may be an important external factor influencing subsequent herbivore impacts on plant species richness. The understanding of herbivore foraging in response to altered plant diversity is important for predicting the roles of herbivores in grassland ecosystem, and for determining the interactive relationship between plant diversity and herbivore foraging, potentially improving the decision making of rangeland people.

The degree of diet selectivity by the herbivore is a critical component of grazing influencing plant diversity (Laca and Demment, 1996). A constant dietary selection pattern by the grazing herbivore may lead to local extinction of preferred plant species, particularly if these species are not dominant or are intolerant of grazing. If however, the grazing selection patterns varied, then the community may remain in a constant state of flux and may reach some dynamic equilibrium, or it may be determined through stochastic events (Newman et al., 1995). Therefore, understanding diet selection patterns and degree of foraging selectivity by the large herbivore are important for conserving rangeland plant diversity and the efficient use of rangeland resources.

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Table 1

Nutritional and chemical characteristics of plant species offered in the feeding experiment (Air-dry matter basis). CP is crude protein; NDF is neutral detergent fiber; ADF is acid detergent fiber; ME is metabolism energy; PSMs are plant secondary metabolites.

Functional group	Plant species	CP (%)	ME (MJ/kg)	NDF (%)	ADF (%)	PSMs
Grasses	<i>L. chinensis</i>	9.26	6.33	69.58	39.42	Few
	<i>P. australis</i>	10.16	6.54	71.26	41.57	Few
	<i>C. virgata</i>	11.82	7.56	65.60	37.70	Few
Legume	<i>L. quinquenervius</i>	14.05	8.71	54.44	39.02	A few
Forbs	<i>K. integrifolia</i>	11.39	8.19	57.28	42.96	A few
	<i>A. scoparia</i>	11.27	9.34	49.47	39.08	Naphtha
	<i>K. sieversiana</i>	12.55	8.63	51.30	29.20	Lycine
	<i>A. venetum</i>	10.24	7.07	38.85	33.85	Flavone

Many factors, such as plant nutrition, flavor, plant secondary metabolite, physical components and sward structure, affect diet selection of herbivore (Cooper and Owen-Smith, 1986; Cooper et al., 1988; O'Reagan, 1993; Edwards et al., 1994; Wang et al., 2010a, 2010b). There has been a large body of knowledge about diet selection strategies of herbivores, and many hypotheses have been invoked to explain patterns of diet selection by herbivores, including diet selection based on intake rate (Owen-Smith and Novellie, 1982), frequency-dependent food choice (Bergvall and Leimar, 2005), a nutritional balance (Westoby, 1978) and detoxification limitation (Freeland and Janzen, 1974), and a learned association according to post-ingestive consequences (Provenza, 1995) etc. Yet, diet selection of herbivore is highly complex, and the foraging environment with which free-ranging herbivores are generally faced is also highly complex. We argue that herbivore might adopt a series of different foraging strategies under conditions of different plant diversity. For example, the post-ingestive feedback has been tested to be an important mechanism by which herbivores make diet selection (Villalba and Provenza, 1996, 2000). Nevertheless, the extent to which the mechanism is important when multiple food options are available, gradually decreasing (Duncan and Young, 2002; Ginane et al., 2005).

In this study, we adopted an indoor feeding trial approach to examine the influence of altered plant species richness and plant functional group composition on the dynamics of diet preference and foraging selectivity by sheep. Our major aim was to reveal sheep diet selection strategies under different plant species composition and diversity conditions and attempt to elucidate ecological consequences of the foraging strategies for grassland plant diversity conservation.

2. Materials and methods

2.1. Herbivores and plant species

The experiment was carried out in July/August 2005. Nine 2-year-old male Northeast Fine-wool sheep (body weight 35.4 ± 1.8 kg, mean $\pm$ SE) were used in this study. The sheep breed is typical of the abundant herbivore livestock throughout northeast China. In the weeks before the experiment, the nine sheep used in the feeding

experiment grazed in native grassland. The plant species used in the feeding experiment are native to and common in the meadow steppes of northeast China. These plant species form the main proportion of sheep diet in this type of rangeland. They comprised eight species from three plant functional groups (grasses, legume, and forbs) with different nutritional value (Table 1). The grasses included *Leymus chinensis* (Trin.) Tzvel., *Phragmites australis* (Clav.) Trin., *Chloris virgata* Sw. with commonly low nutritional value. The legume included *Lathyrus quinquenervius* (Miq. Litv.) with relatively high nutritional value. And the non-leguminous forbs included *Kalimeris integrifolia* Turcz., *Artemisia scoparia* Waldstern et Kitailae, *Kochia sieversiana* (Pall.) C. A. M., *Apocynum venetum* L. with rich plant secondary metabolites (PSMs), especially for *A. venetum* and *A. scoparia*. *K. sieversiana* contains high protein and salt contents besides PSMs. Plants were collected from adjacent grassland and then cut into pieces about 10 cm in length before feeding.

2.2. Experimental design

Four plant species richness levels (2, 4, 6 and 8 species) were created (Table 2). Within each richness level, we replicated three different species combinations (COMB1, COMB2 and COMB3) based on plant functional type (grass, legume or forb, respectively). Overall, there was relatively higher plant functional group richness in COMB3 than in COMB2, and in COMB2 than in COMB1. For example, at 2 species richness level, the plant functional group richness was 1, 2 and 2 for COMB1, COMB2 and COMB3 respectively, and at 4 species richness level, the plant functional group richness was 2, 2 and 3 for COMB1, COMB2 and COMB3 respectively (Table 2). Commonly, there were relatively large differences in nutrient levels and palatability amongst the plant functional types. Thus, the three basic combinations based on plant functional groups provided contrasting diets. For example, the nutritional value of *L. chinensis* and *P. australis* was similar but there were large differences between *L. chinensis*, *L. quinquenervius* and *K. integrifolia*. The order in which species were added was created by using a nested species loss approach (Zavaleta and Hulvey, 2004). Namely, the most abundant and dominant plant species from each of the 3 functional groups in the rangeland were kept in all treatments and relatively rare species were added to raise the level. There were three sheep replications for each species combination (COMB1, COMB2 and COMB3), and each of the nine sheep was given each plant richness level offered for 16 consecutive meals (8 days).

2.3. Feeding and experimental procedure

An indoor cafeteria trial approach was adopted in this experiment. Nine sheep were individually housed in nine 4.2×3.2 m sheepfolds, two weeks before the experiment to allow them to be accustomed to their new environment and the feeding pattern. These sheep had free access to water. Each sheep was offered all plant species simultaneously twice a day at approximately 0730 and 1430 h to provide estimate of preference. Meals were removed after 2 h. Plant species were separately presented to sheep in the

Table 2

Design of the feeding experiments. Plant species are abbreviated as follows: Lc = *L. chinensis*, Pa = *P. australis*, Ki = *K. integrifolia*, Lq = *L. quinquenervius*, As = *A. scoparia*, Ks = *K. sieversiana*, Av = *A. venetum*, Cv = *C. virgata*. Numerical values and titles in brackets are the number and composition of plant functional groups.

Level of diversity	COMB1	COMB2	COMB3
2	Pa + Lc (1, grass)	Ki + Lc (2, grass + forbs)	Lq + Lc (2, grass + legume)
4	Pa + Lc + Ki + As (2, grass + forbs)	Ki + Lc + Pa + Av (2, grass + forbs)	Lq + Lc + Ks + Av (3, grass + forbs + legume)
6	Pa + Lc + Ki + As + Cv + Ks (2, grass + forbs)	Ki + Lc + Pa + Av + As + Ks (2, grass + forbs)	Lq + Lc + Ks + Av + Pa + Cv (3, grass + forbs + legume)
8	Pa + Lc + Ki + As + Cv + Ks + Av + Lq (3, grass + forbs + legume)		

group of troughs with one plant species per container. All troughs were placed close together before each sheep each day. More than enough plant material was added to each trough for the 2 h meal so that 30% or more of plant material in each trough remained at the end of the meals. Each plant species were weighed before and after each meal. Water content of each plant species was measured before and after each meal and a correction was made for water loss. The dry matter mass eaten per meal could thus be calculated.

2.4. Data analysis

Based on the intake of each species in each meal, we calculated each sheep's preference for each species in each meal. Preference was expressed as percentages by dividing intake of each species by the total intake of all species. We first checked meal to meal preference dynamics over the consecutive 16 meals for different species and analyzed the meal to meal variations for preference of each species, respectively, in sixteen meals by computing coefficient of variation (C.V.) of preference for 16 meals at each diversity level. We performed two-way ANOVAs of the C.V. in four richness levels for eight plant species respectively using the individual sheep as block (random factor), plant species richness as a fixed effect, to investigate effects of plant species richness on preference dynamics.

We compared sheep foraging selectivity at different species richness levels. The overall selectivity, as indicated by the difference between the composition of the diet and that of the available plant (Laca and Demment, 1996), was examined. The Overall Selectivity Index (OSI) was determined by the following equation:

$$OSI = \frac{\sum_{i=1}^n (q_i - p_i)^2}{\max_{1 \leq i \leq n} \left\{ 1 - 2q_i + \sum_{i=1}^n q_i^2 \right\}}$$

where p_i is the proportions of the food options consumed per meal, q_i is the proportions of the food options offered, and n is number of species offered. $OSI = 0$ when the same proportions of each food offered are consumed (i.e. completely unselective), and $OSI = 1$ when only one food type is consumed (i.e. completely selective). A repeated-measures analysis of variance was used for the overall selectivity. This ANOVA model contained species richness as the between-subject factor (main effect) and time (meals) as the within-subject (repeated) factor, and individual sheep as block (random factor).

At 8 species richness level, the three species combination treatments (COMB1, COMB2 and COMB3) have identical species composition, and all the eight plant species were offered to the nine sheep (see Table 2). Therefore, we examined the individual sheep variation in OSI at 8 species level. Statistical analysis showed that there was not significant individual sheep impact for OSI. Thus we further analyzed effects of different plant functional group combinations on the foraging selectivity of sheep at 2, 4 and 6 species richness level respectively. Dependent variable of OSI was tested against the independent variable of plant functional group combinations using the General Linear Model Procedure.

All statistical analyses were performed with the SAS 6.12 statistical package. Assumptions of normality and heteroscedasticity were tested. Statistical difference between levels was determined by Duncan's tests. Significance level was set at $P < 0.05$.

3. Results

3.1. Meal to meal variation in diet preference

The results of the selection of plant species by the sheep for each of the 16 meals in three species combinations at four plant species

richness levels showed temporal variation (Fig. 1). When plant species richness was low, the variation in diet selected was relatively small. In contrast, large meal to meal variation occurred when there was a high plant species richness and several plant functional groups in the forage on offer.

To further investigate meal to meal variation in diet preference, we analyzed the CV's for 16 meals for the eight plant species respectively shown in Fig. 2. The CV's of preference for the eight plant species all increased with level of plant species richness and the ANOVA's revealed that these differences were statistically significant (Fig. 2). This indicates that sheep appears to exhibit an increasingly stochastic behavior for diet selection in response to a gradual increase in the number of plant species available, and there are strong effects of plant species richness on temporal pattern of diet preference in sheep.

In order to examine effects of the post-ingestive learning on meal variation in preference, we divided the time series of 16 consecutive meals into four feeding sessions (1–4 meal, 5–8 meal, 9–12 meal and 13–16 meal). Each session is one time step in length. Meal variation in diet preference was analyzed at four feeding sessions respectively. The results showed that, at 2 species, the meal variation of *P. australis* and *L. quinquerivius* declined with experience, and there was no significant difference for meal variation of the other two species among different feeding sessions (Fig. 3). At 4 species, there were not significant differences among the four sessions for meal variations of all the plant species. At 6 species, the meal variation of *L. chinensis* and *A. venetum* increased with experience,

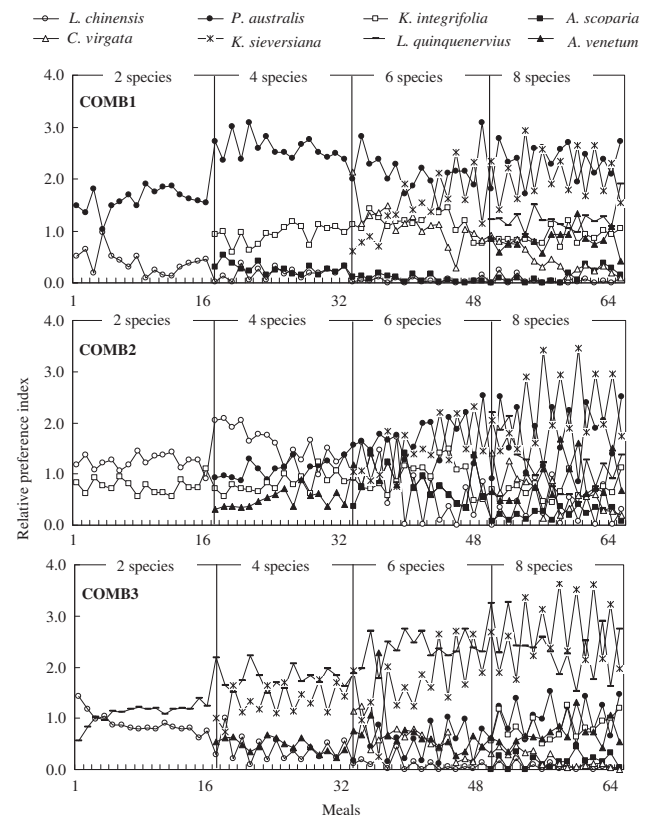


Fig. 1. Sheep diet preference over time (meals) at 2, 4, 6 and 8 species levels and three species combinations (COMB1, COMB2 and COMB3) respectively. At each diversity level, sheep was consecutively fed 16 meals (see Materials and methods). The relative preference index is the proportion of intake (Intake of each species/Total Intake) multiplied by number of species offered (i.e. 2, 4, 6 or 8). Points are the means for three sheep.

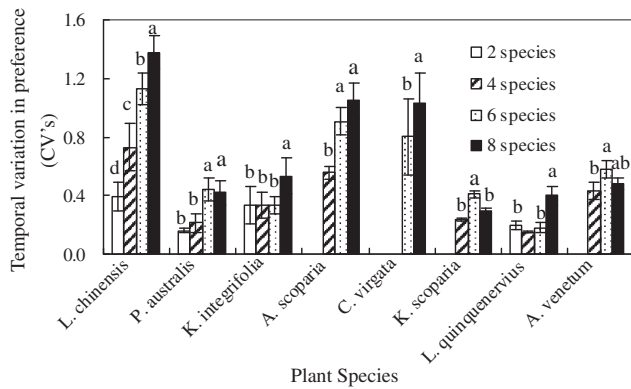


Fig. 2. Coefficient of variation of plant preference for 16 meals for the eight species at 2, 4, 6 and 8 species levels respectively. Values are means of all sheep presented the plant species in the diet over three species combinations. Bars are standard errors. Bars with different letters at different species diversity levels for the identical species are significantly different ($P < 0.05$).

and there was no significant difference for meal variation of the other species among different feeding sessions (Fig. 3). At 8 species, there were significant differences among the four sessions only for meal variations of *K. integrifolia* and *A. scoparia*, but there was not obviously decreasing or increasing trends with experience.

3.2. Foraging selectivity

Overall the ANOVA indicated that plant species richness significantly affected overall selectivity of sheep ($P < 0.05$, Fig. 4). The OSI of sheep at 6 and 8 species richness levels were higher

significantly than that at 2 and 4 species. Specific comparisons among the four plant diversity levels revealed that foraging selectivity of sheep (i.e. OSI) on COMB1 treatments were higher significantly than that on COMB2 and COMB3 treatments for 2 and 4 species richness levels, and no significant difference among the three combination treatments for 6 levels (Fig. 4). The highest selectivity index by sheep (at an Overall Selectivity Index of 0.447) was at the 2 species level of COMB1 (*P. australis* and *L. chinensis*).

4. Discussion

4.1. Effects of plant species richness on diet selection pattern of sheep

We found that the sheep did not usually maintain stable diet selection patterns for the 16 consecutive meals of the plant species combinations offered. This suggests that the sheep modified their diet selection behavior over meals, in most circumstances. The 'temporal' pattern we observed in diet selection of sheep during each set of 16 meals may be explained in two ways. First, the temporal pattern may be attributed to taste or nutrition modulation, and post-ingestive learning (i.e. learned preference or avoidance) (Burritt and Provenza, 1989; Provenza et al., 2003). Empirical evidence indicates that herbivore diet selection or diet preference change as a result of food ingestion, and the degree of change in preference, depends on the nutritional characteristics of the food (Early and Provenza, 1998). Sheep and cattle will seek alternatives to forages they have consumed for several days or hours, and diet selection of sheep has been shown to change within meals (Newman et al., 1994). Second, the variation in meal to meal preferences may also be partly non-deterministic in nature resulting from the inability of herbivores to discriminate among food items (Illius et al., 1999).

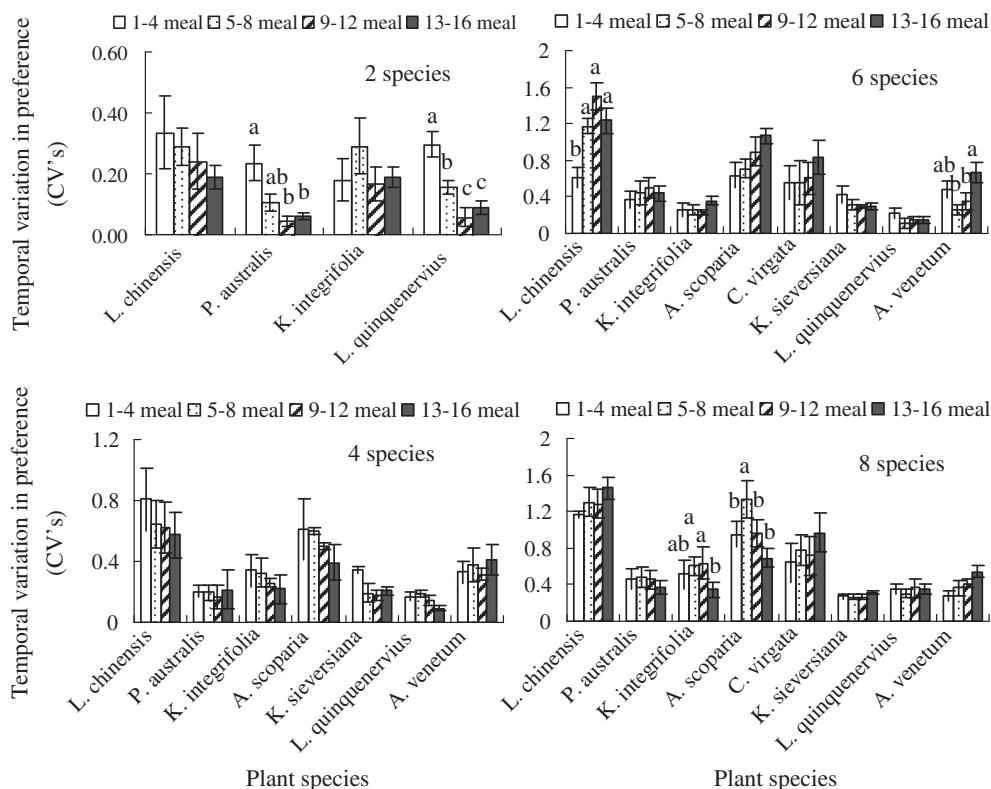


Fig. 3. Meal variation of plant preference at different feeding sessions (1–4 meal, 5–8 meal, 9–12 meal and 13–16 meal) for the eight species at 2, 4, 6 and 8 species levels respectively. Values are means of all sheep presented the plant species in the diet over three species combinations. Bars are standard errors. Bars with different letters at different species diversity levels for the identical species are significantly different ($P < 0.05$).

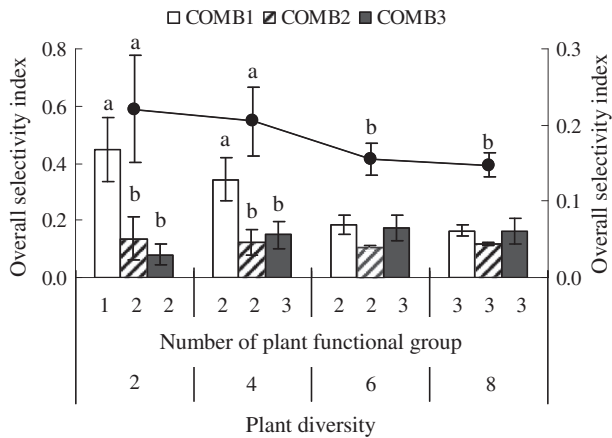


Fig. 4. Foraging selectivity of sheep under different diversity levels and different species combinations. The overall selectivity index is the mean of 16 meals at each diversity level. Histograms represent the mean number of three sheep in different species combinations (values on left axis). Points are means of nine sheep in all combinations (values on right axis). Bars are standard errors.

Interestingly, it was found in this study that the magnitude of variation in diet selection increased significantly with plant species richness, that is, diet selection of sheep shifted between meals more strongly as plant species richness increased. Also, the Overall Selectivity Index of each meal reduced significantly as the number of plant species available increased (Fig. 4). According to optimal foraging theory, an animal should always either eat or ignore a food, and this selectivity of animal may be 'expected' to intensify as the differences among alternatives and the opportunity for selectivity increase (Stephens and Krebs, 1986). Nevertheless, we found that herbivores typically exhibit partial preference and diet diversity not only within meals, but also between meals. We explain changes in diet selection from two perspectives. High plant species richness in food available poses both opportunities and challenges. On one hand, large herbivores have many more opportunities to choose preferred plants and modulate taste and nutrient among plant species, under higher diversity conditions (a wider range of plant species on offer). On the other hand, they are thought to be of poor 'intelligence'. The choices available to herbivores are much more complex under higher plant species richness, and their ability to make 'nutritionally wise' selections may be reduced (Wang et al., 2010b). There is some evidence that herbivores have a limited ability to learn when confronted by a more complex foraging environment (that is, a greater number of plant species) (Duncan and Young, 2002; Ginane et al., 2005). In this circumstance, herbivores may not be able to properly differentiate between the nutritional values of the different species on offer, at a single meal. If this is so, then a larger number of plant species will reduce the ability of an individual herbivore to determine which combinations of species will best meet nutritional needs.

Experimental studies show that animals can associate a food type with its post-ingestive consequence and develop a diet preference in accordance with a beneficial or detrimental post-ingestive consequence (Provenza, 1995; Duncan et al., 2006). Variation in diet preference over time may therefore be a learning process of animal. And the diet preference would shift at first and then stabilize. However, we found that, at 4, 6 and 8 species level, the variation did not decline with increasing time allowed for the same set of choices (Fig. 3). At 2 species level, we found that the meal variation of *P. australis* and *L. quinquerivius* declined with increasing time, but no effects for the *L. chinensis* and *K. integrifolia*. Furthermore, diet preference did not vary significantly over time at

2 species level. Overall, in this study, there was no obvious effect of post-ingestive learning on meal variation in diet preference. We can not determine that whether the 16-meal was long enough to animal learning yet, but, as we know, diet selection in the real world would not present the animal with too long time to confront the same set of species to learn. Rangeland herbivore always lives in a changing world with a complex mix of different food types in time and space.

4.2. Effects of plant functional group composition on diet selection pattern of sheep

Different plant species combinations also substantially influenced the 'foraging' pattern of the sheep. For example, for the combination of two species which differed in functional type [*L. chinensis* (grass) and *L. quinquerivius* (legume) or *K. integrifolia* (forb)], the temporal variation in preference was large, while, for the combination of *L. chinensis* and *P. australis* (both grasses) it was smaller. Different plant functional types usually differ considerably in nutritional characteristics, which would possibly provide a complementary nutritional advantage to the herbivore. The results of the Overall Selectivity Index provided additional evidence for this conclusion. Sheep exhibited low selectivity for the combinations of different plant functional types, and, on average, ingested similar proportions of the plant species on offer (Fig. 4). By contrast, sheep exhibited high selectivity when feeding on a mixture of the same functional types characterized by somewhat similar nutritive value (e.g. *L. chinensis* and *P. australis*) (Fig. 4). A study found that food selection of lambs was explained by nutritional factors of the plants, but when the nutrient content of different species was similar, differences in the flavor of the plant became important as a discriminating factor (Scott and Provenza, 1998). For example, *L. chinensis* and *P. australis* have similar nutritional characteristics, but the latter species has more leaf soluble carbohydrate and therefore a sweeter taste. We suggest that large herbivores will be seeking a variety of plants to ensure a nutrient balance when food on offer has different nutrient profiles, while the focus should be on strongly selecting more palatable forage when forage resources available is similar in nutrient profiles. Therefore, improving plant functional group diversity can reduce herbivore selectivity and promote more uniform use of different plant species in rangeland.

4.3. Diet selection strategies to altered plant diversity and ecological implications

In summary, we demonstrated that sheep exhibit different temporal patterns of preference in response to changes in level of plant species richness. The preference pattern was more deterministic and more constant at low plant species richness, while a more variable pattern was observed at higher plant species richness. This altered preference pattern of herbivores in highly diverse plant communities appears to be a successful (or optimal) foraging strategy, because high herbivore performance is obtained from the higher plant species richness (Wang et al., 2010c).

The behavioral responses of the herbivore under different plant species richness have implications for maintaining plant species richness in rangeland communities. The interaction of plant–herbivore forms a feedback loop. When plant diversity was high, the larger variability of diet preference by sheep and lower selectivity, were beneficial to maintaining high plant diversity. Furthermore, the larger variability of diet preference might improve seed dispersal by herbivores, thereby contributes to plant diversity conservation (Ozinga et al., 2009). Thus, there may be a weak positive feedback between plant species richness and herbivore foraging. We further suggested that pre-grazing plant species richness is an

important external factor influencing subsequent herbivore impacts on rangeland plant diversity, and improving plant diversity, especially for plant functional group diversity, can reduce herbivore selectivity and promote more uniform use of different plant species in rangeland.

Acknowledgment

We thank G. Chen and X. Sun for technical assistance and Z. Abouguedia for suggestions on drafts of this manuscript. This project was supported by the National Key Basic Research Program (2007CB106801), and the National Natural Science Foundation of China (No. 31072070, 31070294) and the State Agricultural Commonweal Project (200903060-2, 201003019).

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