Interactions between Foraging Behaviour of Herbivores and Grassland Resources in the Eastern Eurasian Steppes

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The XX International Grassland Congress took place in Ireland and the UK in June-July 2005. The main congress took place in Dublin from 26 June to 1 July and was followed by post congress satellite workshops in Aberystwyth, Belfast, Cork, Glasgow and Oxford. The meeting was hosted by the Irish Grassland Association and the British Grassland Society.

Proceedings Editor: D. A. McGilloway

Publisher: Wageningen Academic Publishers, The Netherlands

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Key points

1. In rangeland areas such as the eastern Eurasian steppes (Mongolia and China), foraging behaviour is influenced by plant or vegetation properties with high heterogeneity.
2. Until recently foraging theory has not accounted for the foraging process or ingestive behaviour. Existing theories on foraging behaviour need to evolve and begin to coalesce, and combine with observations or manipulative experiments.
3. Plant and patch properties such as diversity and height influence animal foraging behaviour (related to foraging process or diet selection) in heterogeneous steppes.
4. Stocking rate is the most important management factor for grazing or vegetation management, and determining the optimal stocking rate in steppes depends upon variable annual forage production, vegetation regrowth and animal production targets.

Keywords: animal-plant interactions, stocking rate, heterogeneity

Introduction

Rangeland areas comprise 25% of the world's grassland (Hodgson, 1990), and are found in prairie, pampas, veld and campos, savanna, and steppe. This paper will focus on the latter, located within the Eurasian continent ranging from Ukraine to Kazakhstan, Russia, Mongolia and China (35-57^{o}N). Although steppe landscape is greatly modified by human activity, it is still the climax vegetation existing over a range of climates from continental to arid and semiarid climate (annual precipitation = 200-450 mm) (Zhu, 1993). The eastern Eurasian steppes are located on the Mongolian Plateau and Songliao Plains (in Mongolia and China) with three zonal types including 'meadow steppe', 'typical steppe' and 'desert steppe' (Wu, 1990). The dominant species influenced by climate or grazing are *Stipa* and *Leymus* genus (*Stipa baicalensis*, *S. grandis*, *S. breviflora, S. kelemenzii* and *Leymus chinensis*), and forbs such as *Artemisia frigida* and *Filifolium sibiricum*. Each type of steppe plays an important role in animal production, providing over 90% of the food source for maintaining basic requirements of herbivores. Critical problems facing farmers include how to avoid or reduce overgrazing and how to enhance forage availability or grazing efficiency within the highly heterogeneous steppes.

The ecological relationship or interaction between plant and animal is universal, and of fundamental importance (Howe & Westley, 1988). Herbivores interact with plants to maintain their requirements for growth and reproduction, but the availability of plants also regulates the dynamics and production of animal populations. Herbivores play a role in controlling the function of whole ecosystems, and show an asymmetry in the interaction of plant and herbivore (Crawley, 1983). The plant-animal interface is a fundamental interaction between trophic levels, and is the central feature of natural and artificial grassland ecosystems (Ungar, 1996). A better understanding on how animals can effectively exploit plants, and how plants alter their fitness and adaptive strategies in response to animal foraging will provide a baseline for the sustainable utilisation of grassland resources for animal grazing. Theoretical models on the interaction of plant and herbivore lay a foundation for interpreting mechanisms of co-evolution between plant and animals in nature (Belovsky *et al*., 1999; Loeuille *et al*., 2002).

Two important research aspects for interactions between plants and animals in grasslands are: i) grazing intensity, i.e. how herbivores exploit plants, and ii), herbivore behaviour, i.e. individual animal performance. These are considered the most direct ways that grazing animals interact with a plant community (Newman *et al*., 1995). Previous studies concentrated on the effects of herbivore grazing intensity (stocking rate, carrying capacity) (Heady & Child, 1994; Roe, 1997). Current interest lies in determining the relationship between herbivore behaviour and vegetation property. However, it is necessary to consider grazing intensity and animal behaviour synchronously within the context of plant and herbivore interactions. Herbivores interact with foraging plants at multiple levels in grasslands. Grazing intensity embodies the circumstance at a higher level (herbivore group or population effect), whilst at a lower level foraging behaviour is often 'individual-dependent'. Thus, the interaction between animal and plant can be summarised by relationships of grazing intensity and plant regrowth, and of foraging behaviour and spatial vegetation pattern (heterogeneous characteristics of vegetation) within grazing systems.

In this paper, experimental results on foraging behaviour especially diet selection, and the relationship between stocking rate and vegetation regrowth on 'natural steppes' in the eastern Eurasian steppes are presented. Existing theories on foraging behaviour of herbivores are reviewed.

The foraging process and its theoretical basis

Foraging process

The foraging process can be divided into two phases: decision-making (searching), and intake or ingestion (cutting, chewing, swallowing and digesting) (Ungar, 1996; Manning & Dawkins, 1998). Decision-making exhibits variable time scales (i.e. second to second). The ingestion phase, during which animals obtain energy or nutrients, follows each decision-making event. Most studies on foraging process focus on the former phase (Bazely, 1990; Howery *et al*., 2000). Distinguishing the two phases by time sequence is difficult because animals may determine their foraging direction during ingestion. It is possible that different mechanisms drive the two phases. An animal's learning and experience (cognition), and biological innate potentials play major roles in decision-making and ingestion, respectively (Bailey *et al*., 1996). This hypothesis, however, remains to be tested. For the whole foraging process, components such as decision, currency and constraint should be considered to determine mechanisms related to foraging behaviour.

Theories on foraging process

Rules-of-thumb

Simple Rules-of-Thumb (RT) have been used to describe foraging and behaviour. For example, Iwasa *et al*. (1981) used the number, time, and 'quitting time' of animal foraging when herbivores were facing different food distributions on patches. Rules of thumb can provide a primary understanding of foraging decision or diet selection of herbivores in heterogeneous grasslands, and are an option where the time or effort to obtain information is prohibitive (Ward, 1992; Bailey *et al*., 1996). The RT hypothesis has several limitations, for example, it is difficult to explain foraging 'optimal' solution using RT for homogeneous environments with no food differences. In addition, it is unclear whether RT can play a role in foraging selection when animals have basic perception and spatial memory. There is also a lack of experimental evidence to verify this hypothesis.

Marginal value theorem

Marginal value theorem (MVT) was developed by Charnov (1976), and has been used to describe foraging strategy when animals exploit 'patchy' resources. The food quality of a patch, residence time within the patch, moving time between patches (departure), and foraging energy are useful parameters explaining the foraging decisions of animals. However, several experiments have shown that measured values such as residence time and intake rate, is often lower than that predicted by MVT, even though the behaviour of small herbivores such as insects fits MVT (Roguet *et al*., 1998; Prache & Peyraud, 2001). The disadvantage of MVT is that it was hypothesised that the forager could not accumulate information on patches, whereas there is experimental evidence to suggest that both cattle and sheep can accumulate experiences of patch characteristics (Edwards *et al.*, 1996; Bailey *et al.*, 2000).

Optimal foraging theory

'Optimal foraging theory' (OFT) is useful in situations when a forager makes decisions about current resource consumption based on tradeoffs in resource attributes (Gerber *et al*., 2004). It provides a functional approach for examining grazing behaviour (Bailey *et al*., 1996) and can quantitatively account for the foraging decisions of animals (Stephens & Krebs, 1986). Maximisation of energy intake rate and minimisation of the time necessary to obtain nourishment are two measures of foraging success that remain in standard use. Foraging success is assumed commensurate with animal fitness (Perry & Pianka, 1997). However, it needs to be developed with more manipulative experiments in both the laboratory and the field (Perry & Pianka, 1997). Optimal foraging theory may be an over-simplified representation of the reality (Prache & Peyraud, 2001). For example, maximisation of reproductive fitness has been simplified into, maximisation of various surrogate currencies such as rate of nutrient intake and energy, because measuring fitness is difficult or impossible in most cases (Lemon, 1991). Nutrient balance seems to be more important than energy intake for herbivores, even in poor food environments where animals have to forage on plant species with a low frequency distribution, and reducing their mean energy intake efficiency, while OFT only emphasizes net energy (nutrient total) or fitness.

Theory of minimal total discomfort

The theory of minimal total discomfort (MTD) was proposed by Forbes (1999, 2001), and is based on the physiological state of animals. A total 'discomfort signal' (factor) integrated from metabolisable energy (ME), crude protein (CP) and neutral detergent fibre (NDF) was used as a parameter estimating animal's foraging behaviour. Animals tend to reach the state of MTD during feeding or the foraging process, and so alter intake or food selection so as to minimise total discomfort (Figure 1). This model suggests that food choice is a physiological requirement, and is related to energy intake and nutrients. However, determining discomfort components is difficult and no information exists on the spatial location of animals during the foraging process.

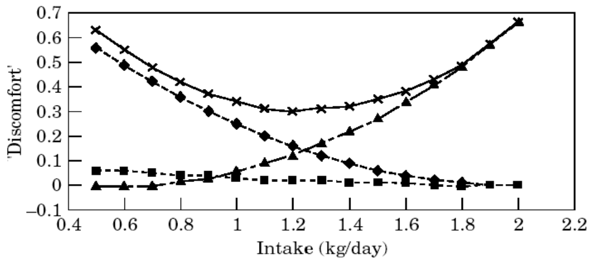

Figure 1 Relationships between intake and nutrient components in an animal diet (♦=ME; ■= CP; ▲= NDF; ×= Total) (Forbes, 2001)

Among the current foraging theories or hypothesis, a universal model than can explain the foraging process as a whole is lacking. Future studies on animal physiological state, learning and experience, and environmental constraints should be conducted to verify many of these hypotheses. A better integration between decision-making and intake, and the development of improved elementary components may help unify these hypotheses.

Foraging behaviour and plant and patch characteristics of steppes

The patch is considered as a cluster of one or more plant species with high density, and also as a basic foraging scale (i.e. the level of variability encountered within a landscape unit) (Wallis de Vries & Daleboudt, 1994; Bailey *et al*., 1996; O'Reagain, 2001). Natural 'meadow steppe' vegetation of North-eastern China has a higher heterogeneity than that of managed grasslands, so foraging behaviour needs to match this variability.

Plant and patch location (decision-making) for herbivores

Plant and patch decision-making implies that herbivores forage directionally. It is often assumed that herbivores tend to graze patches prior to individual plants because patches contain a greater amount of nutrient and energy, but a shift in food location may occur when mixed or mosaic food distribution is encountered in heterogeneous grasslands. What factors influence herbivores food location? Controlled experiments in natural 'meadow steppes' were conducted in 2004 with yellow cattle to address the effect of various factors on herbivore's food location.

In the experiment, four cattle grazed for 10 minutes in different paddocks (paddock area = 600m^2) with patches and randomly distributing plant individuals (dominant species was *Phragmites communis*). The cattle displayed a strong preference for patches compared to plant individuals Table1). Moreover, the size of the patch was positively correlated to herbivore foraging time. Foraging time on patches increased considerably when patch size reached 50m^2. When patch size was small (10m^2), it was difficult for cattle to locate a food patch. Previous experiments have shown that herbivores have the ability to remember spatial location of food patches (Edwards *et al*., 1996; Sibbald & Hooper, 2003) and can learn to associate visual cues with disparate food quality, and use this information to forage more efficiently (Howery *et al*., 2000). Results from limited experiments of food location imply that a shift of foraging level from plant to patch copes with the size, number and quality of patches.

Table1 Foraging time of yellow cattle at individual plant and patch scales (patch treatments: size and number) in meadow steppes of northeastern China (mean ± sd)

Foraging time (s)	Paddock number and patch size (m^2)				
	P1 (0 m^2)	P2(10 m^2)	P3(50 m^2)	P4(100 m^2)	P5(160 m^2)
At individual plant	401 ± 56	300 ± 50	155 ± 64	27 ± 13	10 ± 7
At patch		107 ± 39	336 ± 34	469 ± 14	474 ± 26
Foraging time (s)	Paddock number and (patch number)				
	P1 (2)	P2 (3)	P3 (4)	P4 (5)	
At individual plant	369 ± 56	72 ± 33	121 ± 33	38 ± 14	
At patch	81 ± 26	191 ± 38	195 ± 50	197 ± 51	

Influence of plant and patch on herbivore diet selection

Effect of plant diversity on intake

Vegetation in 'meadow steppes' is diverse with over 30 plant species that provide food for grazing sheep or cattle to meet their physiological requirements. In these conditions herbivores are better able to meet their dietary needs and mitigate against toxins in their intake compared to exploiting a single food source. An experiment with increasing plant species and free choice for sheep showed that sheep preference was strongly correlated to plant diversity (Figure 2).

Average daily intake of sheep was 603.7g when a single plant species (*L. chinensis*) was offered, but it increased significantly to 823.5g when four plant species were fed. Little further increase was found when the number of species increased to nine. The strong correlation between animal selection and plant species incidence was reported in a Sicilian pasture (Carpino *et al*., 2003). Provenza *et al*. (2003) reviewed the relationships between herbivore's diet and plant biochemical diversity, and concluded that foraging diverse plant species would benefit nutrient balance and limit toxins in food. It is suggested that diverse foraging could improve satiety and modulate taste for herbivores, and stimulate the ingestion of more food. Diverse foraging in natural steppes with low vegetation production may be valuable for vegetation production and ecosystem stability during the co-evolution between plants and herbivores, because diverse foraging can help maintain high regrowth potential and species diversity of the entire community.

Vegetation (patch) height selection

Vegetation height (sward or patch surface height) is used as an indicator for plant growth and production, herbage allowance, and is a useful parameter for grazing management (Hodgson, 1981). Many grazing experiments have been conducted on artificial grasslands to determine the relationships among sward height, foraging behaviour, and defoliation pattern (Amstrong *et al*., 1995; Barrett *et al*., 2001; Tharmaraj *et al*., 2003; Wang D. *et al*., 2003).

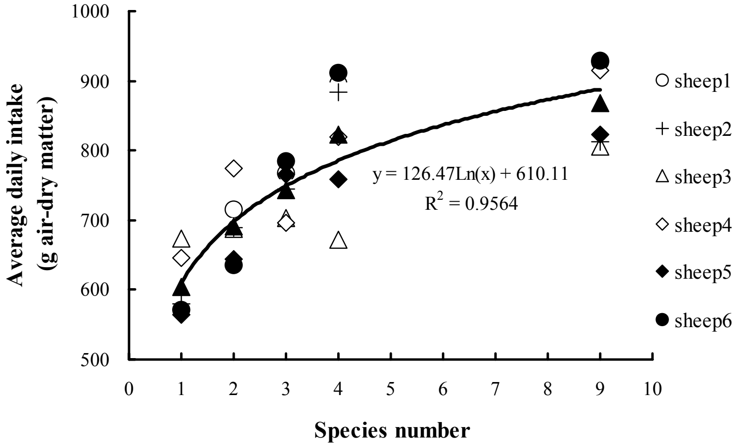

Figure 2 Change in intake for sheep with an increasing number of alternative food sources. Sheep were fed with different combinations of plants (treatment level: 1, 2, 3, 4, 9 species; six replications). Daily intake mass was enough for each sheep and the feeding duration was 15 days.

The heterogeneity of vegetation in meadow steppes has a great impact on herbivore's diet selection, expressed as average bite depth (Figure 3) (Wang X. *et al*., 2002). Goats prefer a certain height of vegetation (20-25cm) and this preference remains unchanged during the grazing season. Vegetation height selection for herbivores indicates that there is a trade-off between energy and nutrient for herbivore foraging. When goats graze on patches with tall plants, a greater herbage allowance can be consumed or grazing time reduced.

Most patches with tall plants tend to be comprised of mature plants, thus the higher proportion of reproductive shoots and lignin content would adversely affect digestion and actual plant availability. On the other hand, goats can spend more time and energy obtaining food in lower height patches with higher carbohydrate and protein but lower lignin contents. The consistent trend of patch height selection during the full grazing season suggests that there is a greater intake mass (energy) requirement during early season grazing (less vegetation production) and a greater nutrient preference during late grazing season (adequate vegetation production).

Patch property affecting herbivore intake

Patch characteristics such as the quantity (biomass, height, density) and quality (nutrient-proportions of vegetative shoot/reproductive shoot, legume/grass, and digestive energy and toxin) influence intake, bite dimensions, and animal production (Bailey, 1995; Dumont *et al*., 1995; Distel *et al*., 1995; Prache & Peyraud, 2001; Griffiths *et al*., 2003). However, in natural meadow steppes with high heterogeneous patches, patch height, but not mass and tiller density, are important factors affecting cattle behaviour, with a positive correlation between height and foraging time (Figure 4c). Bite rate of cattle did not vary with patch properties (Figure 4).

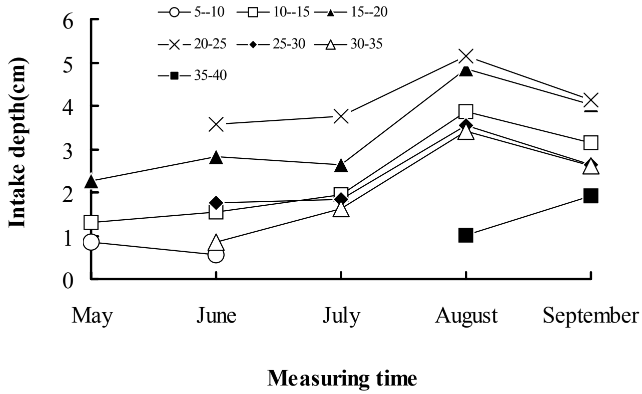

Figure 3 Variations in seasonal bite depth of goats with average vegetation (patch) height. Symbols indicate vegetation heights at 5 cm increments. (Experiment, involved grazing twenty sheep for six months in 'meadow' steppe dominated by *L. chinensis* (Wang D. *et al*., 2002; Wang D., 2004).

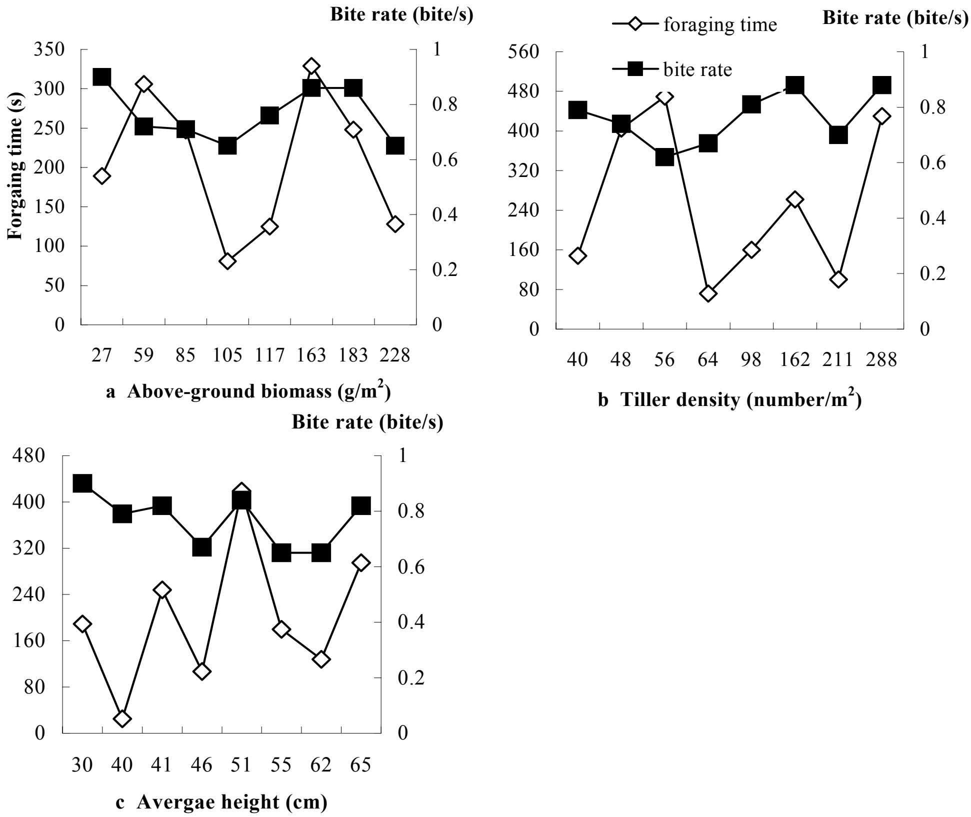

Figure 4 Relationships between patch properties (a, above ground biomass; b, tiller density; c, height) and cattle behaviour (foraging time and bite rate) on meadow steppes. Grazing time was 10 mins. with six replications for the experiment.

Studies on foraging behaviour can be at different scales of plant, patch and vegetation. Previous studies have focused more on ingestive behaviour such as instantaneous intake rate, and less on the digestive process during and after ingestion (O'Reagain, 2001). However, foraging optimisation may be better achieved within a long-term framework including digestion, which involves physiological state, experience, social organisation (grazing spatial distribution), and patch property. Herbivores often have to make trade-offs between foraging behaviour and social behaviour, quality and quantity of patch, and energy intake and time spent grazing. It may be that foraging can only be optimised with some constrains or trade-offs.

Intake of herbivores within intermediate time scale

Intermediate time is defined as the intermittent temporal scale distinguishing short term (second, minute) and long time (month, year). Although sheep tend to choose diverse plant species in steppes, actual species selection is usually concentrated on four or five plant species (Figure 2). During a 12-day experimental period, preference followed *P. tenueoflora* > (*L. chinensis* = *Ph. communis*) > *Kelimeris integrifolia*. This preference was displayed on a daily basis. The two species in the intermediate preference group inter-compensated in the sheeps diet (Figure 5).

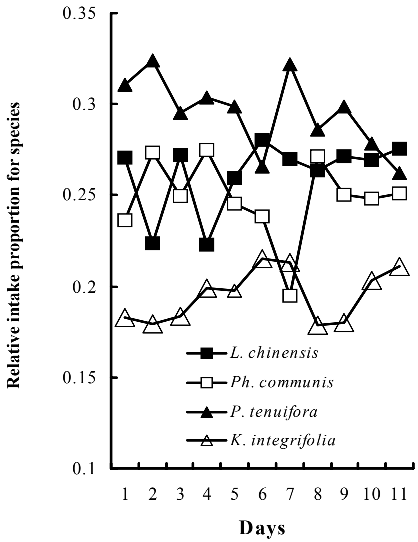

Figure 5 Daily variation in sheep-diet selection for four plant species. Sheep were fed combinations of four common plants in meadow steppes. Daily intake mass was enough for each sheep and the feeding duration was 15 days

An empirical assumption is that the inter-compensation of the two species could meet the needs of daily intake mass (half of total mass in this experiment), but it is unclear whether the displacement and transition of preference between the two species every two or three days can provide essential nutrient balance or need of food stimulus to maintain sheep's preference. The diversity of diet composition for herbivores benefits not only intake mass but also the consequence of intake or preference because of an interaction between nutrient and plant secondary metabolites (PSM) (Villalba *et al*., 2002). However, further experiments on plant nutrient and PSM, and herbivore nutrient intake and metabolism are needed to address this.

Stocking rate of herbivores and vegetation regrowth

There exists a close relationship between vegetation regrowth and stocking rate (Li *et al*., 1997; Kowalenko & Romo, 1998; Wang D. *et al*., 2002). Regrowth derives from the production of new leaves of vegetative tillers, or new tillers produced either from buds on the shoot apex, or rhizome nodes situated at ground level (Davies, 1988). Regrowth is affected by grazing intensity and increasing stocking rate can enhance average leaf elongation and appearance rates and reduce senescence rate of dominant grasses in steppes (Liu Y. *et al*., 2001, 2003). Another characteristic of plant regrowth in response to stocking rate can be expressed as tiller density and the related bud bank of plant population.

Generally, the contribution of tiller number to plant regrowth varies with time of the year, and maintains a certain pattern within the defoliation system. Vegetation tiller density can be stimulated to some extent (Liu Y. *et al*., 2002; Wang S. *et al*., 2003). Variations in tiller density under grazing disturbance may be attributed to triggering tiller bud expansion, which leads to compensatory growth. An observation on the bud bank of *L. chinensis* population under different stocking rates illustrates that grazing directly influenced the number of active buds on rhizomes and intermediate grazing maintained a higher level of active buds (Figure 6).

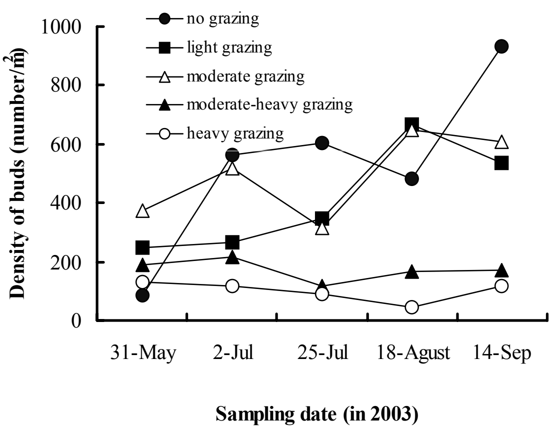

Figure 6 Seasonal bud bank of *L. chinensis* populations as affected by grazing intensity in meadow steppes

Plant regrowth post grazing is a complicated physiological process that involves carbon and nitrogen storage and remobilisation. It is known that water-soluble carbohydrate (WSC) and not carbohydrate concentration in stubble at the time of defoliating, plays the major role in plant regrowth (Volenec, 1986; Fulkerson & Slack, 1994). Work by the authors indicates that there is considerable variation in WSC of basal stems but not in WSC of leaf and root for *Ph. communis*, *P. tenuifora* and *L. chinensis* (Liu J. *et al*., 2003). Nitrogen contents of leaf, stem and roots were not significantly different among defoliation intensities (Liu J. *et al*., 2003). However, carbohydrate or WSC storage alone was not sufficient to explain the amount of regrowth because there was an interaction between carbon and nitrogen recycling during the regrowth of defoliated plants (Lemaire & Chapman, 1996; Thornton *et al*., 2000). Further experiments examining the interaction between carbon and nitrogen metabolism, and quantifying remobilisation will be necessary to fully understand the physiological basis of regrowth post defoliation.

Optimal stocking rate and vegetation production

In China, where there is no standardised grazing capacity for grassland management, stocking rate is the most important management factor. The principal consideration for any rangeland grazing system is to balance livestock needs with the available forage supply through proper stocking rates.

Stocking rate affects standing crop (yield) and net primary productivity. Standing crop of *S. breviflora* desert steppes in Inner Mongolia was 78% higher under moderate as opposed to heavy grazing, and 90% higher under light than under heavy grazing (Liu *et al*., 1996). During the growing season net aboveground productivity was 635, 580, and 535 kg/ha under light, moderate, and heavy grazing respectively (Han *et al*., 1999). Light or moderate grazing in typical steppes is beneficial to forage production especially in dry years.

Heavy stocking rates lower animal liveweight production compared to moderate or light grazing. In a sheep grazing experiment on typical steppes of the Mongolian Plateau, average liveweight gain was 19.4, 15.6 and 11.8 kg/sheep when stocked at 0.68, 0.94 and 1.5 sheep/ha per year (Wei & Han, 1995). Losses due to sheep death were also higher under heavy grazing than under moderate and light grazing (sheep death numbers were 7, 1, and 0 sheep after 5 years heavy, moderate, and light grazing, respectively. The higher sheep mortality in heavy and moderate grazing is due to shortage of forage supply caused by stocking rate in winter and spring seasons.

Liveweight gain was 28.2 and 13.6% higher under light and moderate than under heavy grazing, respectively (Wei & Han, 1995). Liveweight gain per animal and per area unit was affected differently by stocking rate. Even though productivity per animal unit declined as stocking rate increased, productivity per area unit increased up to a point. When grass supply became limited, productivity per unit area then decreased. This is why most ranchers and local people often favour heavy grazing.

It is not possible to achieve both maximum gain per animal and per unit area concurrently. The curves of gain per animal and per unit area cross at the 'peril point' (Figure 7). At this point stocking rate is considered optimal for animal production. For *S. breviflora* desert steppe, the optimal stocking rate equates to a moderate grazing pressure. Therefore, curves of liveweight gain per animal and per unit area can be used to determine the optimal stocking rate in steppe zones of China (Han *et al*., 2000).

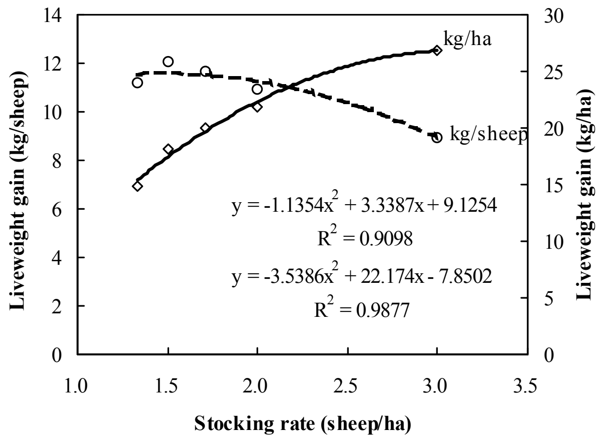

Figure 7 Changes in sheep liveweight gains with different stocking rates in *S. breviflora* desert steppe

Stocking rate or carrying capacity

Stocking rate should match the carrying capacity of grassland for grazing management to maintain its sustainability (Heady & Child, 1994). Long-term data of forage production can be used to calculate the carrying capacity of steppes. Primary production in Inner Mongolian steppes varies with season and year because of the fluctuation in temperature and precipitation (Figure 8) (Han *et al*., 2001). Thus, carrying capacity of steppes varies with forage production. Stocking rate can be either flexible or fixed. Ideally, flexible stocking rate can meet fluctuations in forage production in different seasons and years, but is difficult in practical farming since every farm has a relatively stable livestock number. However, Martin (1975) reported that 90% of proper fixed stocking rate had good results in southern Arizona grasslands.

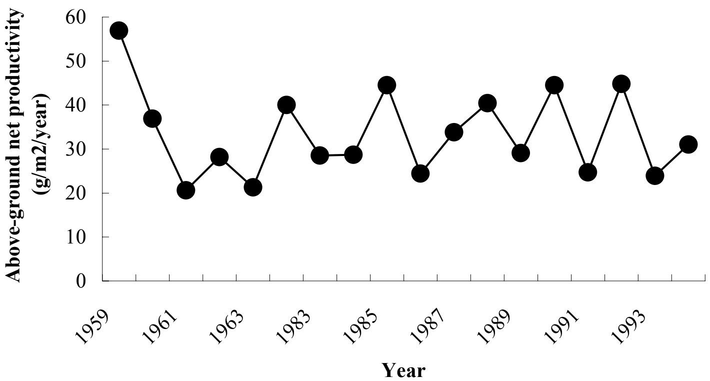

Figure 8 Yearly variation in above-ground net primary productivity of *S. kelemenzii* desert steppe

In conclusion, a series of experiments were conducted to investigate herbivore behaviour and the interaction between herbivore and plant or vegetation at various scales in the eastern Eurasian steppes. The studies on heterogeneous natural steppes produced some unexpected results and may provide new knowledge on the understanding of animal foraging behaviour which will benefit grassland management in the steppes of China, Mongolia and other countries

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