



## High plant diversity stimulates foraging motivation in grazing herbivores

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### Abstract

One of the main challenges of studying grazing ecology is to predict food intake of herbivores. Plant species diversity may have important consequences for regulation of food intake by generalist herbivores. To reveal the regulation processes underlying food intake affected by plant species richness, we investigated sheep foraging during a 2-h foraging period (subdivided into four 30-min intervals) in response to altered plant species richness (2, 4, 6, and 8 species) using an indoor cafeteria trial. Our results showed that high plant diversity significantly improved a sheep's intake during each of the time intervals, and the extent of improvement for intake gradually strengthened as foraging proceeded. Furthermore, we found that dynamics of food intake was modified as plant species richness increased. At lower plant diversity, intake of sheep was highest at the beginning and then decreased continuously as satiation proceeded. But this decreasing trend gradually slowed as the available plant diversity increased, and sheep even maintained high and constant intake during all intervals for the 6 and 8 species level. Fasting is generally thought to be an important endogenous factor affecting herbivore foraging motivation, and effects of fasting decreased as satiation proceeded. Our study indicated that diet diversity could be an important exogenous factor, and the diversity effects significantly increased with time. The complementary effects of endogenous and exogenous factors resulted in high herbivore intake during the entire 2-h grazing bouts under conditions of high plant diversity. We concluded that diet diversity can greatly increase foraging motivation of sheep, and improving foraging motivation, especially at the later phase of the meal, seems to be a key factor for stimulating food intake by the herbivore. Our study also indicates that conserving grassland plant diversity is critically beneficial not only to plant productivity, but also to animal productivity.

### Zusammenfassung

Eine der Hauptaufgaben bei Untersuchungen zur Weideökologie ist die Vorhersage der Nahrungsaufnahme von Herbivoren. Die Pflanzendiversität kann wichtige Konsequenzen für die Regulation der Nahrungsaufnahme durch generalistische Herbivoren haben. Um die Regulationsprozesse aufzudecken, die der Nahrungsaufnahme in Abhängigkeit von der Pflanzendiversität zugrunde liegen, untersuchten wir die Nahrungsaufnahme von Schafen während zweistündigen Fütterungsperioden (die in 30-Minuten-Intervalle unterteilt waren) in einem Indoor-Cafeteria-Experiment mit variierender Pflanzenartenzahl (2, 4, 6, 8 Arten). Unsere Ergebnisse zeigten, dass hohe Futterpflanzendiversität die Nahrungsaufnahme der Versuchstiere während eines jeden Intervalls signifikant verbesserte und dass das Ausmaß der Verbesserung graduell mit zunehmender Fütterungsdauer zunahm. Darüber hinaus fanden wir, dass die Dynamik der Nahrungsaufnahme sich mit zunehmender Futterpflanzenzahl

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änderte. Bei geringer Pflanzendiversität war die Nahrungsaufnahme der Schafe zu Beginn am höchsten und nahm kontinuierlich mit zunehmender Sättigung ab. Aber diese abfallende Tendenz wurde mit zunehmender Futterpflanzendiversität geringer, und die Schafe behielten sogar bei sechs und acht Pflanzenarten eine konstante Aufnahmerate über den gesamten Fütterungszeitraum bei. Fasten gilt allgemein als wichtiger endogener Faktor, der die Motivation zu Fressen beeinflusst. Die Effekte des Fastens nahmen ab, indem die Sättigung fort schritt. Unsere Studie zeigte, dass die Futterdiversität ein wichtiger exogener Faktor sein kann und dass Diversitätseffekte signifikant mit der Zeit zunahm. Die komplementären Effekte von endogenen und exogenen Faktoren resultierten in hoher Nahrungsaufnahme über den gesamten zweistündigen Fütterungszeitraum hinweg, wenn die Futterdiversität hoch war. Wir schlossen, dass die Futterdiversität die Freßmotivation der Schafe erheblich steigern kann und dass die verbesserte Motivation, insbesondere in der späteren Phase des Mahls, ein Schlüsselfaktor für die Nahrungsaufnahme der Herbivoren zu sein scheint. Unsere Untersuchung zeigt auch, dass die Erhaltung einer hohen Pflanzendiversität in Grasländern von entscheidendem Vorteil ist: nicht nur für die Pflanzenproduktivität sondern auch für die Produktivität der Tiere.  
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## Introduction

Explaining and predicting food intake of grazing herbivores has been generating a large amount of research interest in the fields of grassland grazing ecology. The relationship between food intake by herbivores and forage characteristics such as plant structure, morphology, primary and secondary chemistry, density, height, availability and spatial distribution have been well established (Bergvall & Leimar, 2005; Illius & Gordon, 1991; Owen-Smith, 1996; Wang et al., 2010a; Wilmshurst, Fryxell, & Pablo, 1999). However, it is important to note that herbivore consumption of a forage species not only depends on the characteristics of that species, but also on the characteristics of other species in the sward (i.e. context of the plant) (Bergvall, Rautio, Kesti, Tuomi, & Leimar, 2006; Milchunas & Noy-Meir, 2002; Wang et al., 2010b) because of the interactions between nutrients and toxins (Provenza, Villalba, Dziba, Atwood, & Banner, 2003; Provenza et al., 2007; Wang, Wang, He, Liu, & Hodgkinson, 2010c; Wang, Wang, Liu, Huang, & Hodgkinson, 2011), and sensory-, nutrient-, and toxin-specific satiety (Provenza, 1995). Therefore, herbivore consumption is not a function of the characteristics of single plants. Plant species diversity may have important consequences for regulation of food intake by generalist herbivores.

In general, however, there seems to be a lack of studies on relationship between food intake and plant species diversity. Grassland food supply may be highly variable spatially and temporally, and in quantity and quality. Undoubtedly, the grazing animals have many more opportunities to choose the preferred plants and optimize nutrient intake when plant species richness is higher. High plant species richness of grassland communities simultaneously poses challenges to large herbivores. Herbivores may have limited ability to learn when several food types are available simultaneously (Duncan & Young, 2002; Ginane, Duncan, Young, Elston, & Gordon, 2005). Based on studies on acquired aversions to food ingested by herbivores, it has been suggested that providing a variety of forage species may increase herbivore food

intake (Early & Provenza, 1998; Provenza, 1996; Provenza et al., 2009). The few empirical studies on effects of diet diversity on consumption by generalist herbivores only compared the extremes; single species with mixed species (Burritt & Provenza, 2000; Cortes, Damasceno, Jamot, & Prache, 2006; Ginane, Baumont, Lassalas, & Petit, 2002; Marsh, Wallis, McLean, Sorensen, & Foley, 2006). For example, Marsh et al. (2006) compared the intake of possums offered a choice of diets containing different PSMs with that of possums on a diet containing a single plant secondary metabolite (PSM), and found that possum can eat more by selecting mixed diets with a diversity of PSMs that make full use of their detoxification potential. Ginane et al. (2002) also showed that giving the animals a choice between two hays can stimulate their daily intake by at least 10% compared with what was eaten when the same forages were offered alone. It can be conceived that herbivores will eat less of a single species diet than a mixed species diet because of monotonous flavor and nutrient or toxin limitation. A convincing empirical support for the argument was from our recent work (Wang et al., 2010c), which showed the strong asymptotic relationship between plant species richness and voluntary daily intake by grazing sheep. However, still it is not clear how the variety of plant species regulates an animal's motivation to eat and ultimately its total food intake.

Herbivore food intake generally is considered as an outcome of the animal's internal state and 'constraints' arising from the environment. The main characteristics of foraging behavior of herbivores in the short term have also been described in terms of the satiation process and motivation to eat (see reviews by Baumont, Prache, Meuret, & Morand-Fehr, 2000). The linking of instantaneous foraging decisions with satiation processes together with the animal's motivation to eat will contribute to better understand the variation in daily intake by animals (Prache & Peyraud, 2001). Meal eating behavior is the most variable of intake control mechanisms (Abijaoudé, Morand-Fehr, Tessier, Schmidely, & Sauvans, 2000; Gill & Romney, 1994). To reveal the regulation processes underlying food intake by plant species

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