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Diet Selection and Foraging Behavior of Cattle on Species-rich, Japanese Native Grasslands

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Abstract

In addition to serving as livestock pastures, grasslands create wildlife habitats, provide recreational opportunities, and play a key role in watershed regulation. In herbivores, diet selection can profoundly affect the intake of nutrients (e.g., energy, protein and minerals), plant secondary metabolites and toxins. Spatio-temporal heterogeneity in the use of pastures by herbivore livestock means diet selection can also affect vegetational change found on grasslands. In extensive grazing systems, an understanding of this plant-animal interaction is vital for managing animal production and welfare, and ensuring the sustainable use of plant resources. The two goals of this review are to summarize findings regarding diet selection in cattle grazing on Japanese native grasslands and to discuss factors affecting selective grazing of cattle in terms of chemical and behavioral factors. Previous studies showed that Japanese native pastures were composed of 14 to 118 plant species in any given season, of which cattle graze on 22.9–87.5%. Regression analysis showed a strong relationship ($P < 0.001$) between the number of plant species in the diet of cattle and the number of species available, with cattle consuming on average 57.9% of the plant species present. Japanese plume-grass (*Miscanthus sinensis*) is one of a particular favorite species, but the underlying mechanisms remain unclear. Among chemical and behavioral factors, bite size significantly related to relative preference (RP) for native plant species. In contrast, both nutrient concentrations and other chemical compounds that affect taste and smell failed to explain RP for native plants. Recent research has shown that the vertical distribution of available leaves

is another key factor affecting foraging behavior in cattle. These findings warrant further study of the diet selection mechanism as a complex of chemical-behavioral response.

Introduction

Grasslands are important for grazing livestock. They are also valuable as wildlife habitats, recreational lands, and areas that help regulate watersheds (e.g., WalisDeVries et al., 1998; Willms and Rode, 1998; Shimoda, 2010). While 65% of Japan's land area is covered by forest, grasslands account for a mere 2.2%. This small proportion of the land area provides habitats for unique wild animals (Sugiura, 2004). *Miscanthus sinensis* (Japanese plume grass) and *Zoysia japonica* (Japanese lawn grass) are two of the major species that dominate in these grasslands, and both have long served as cattle grazing pasture (Ogura et al., 2004).

Livestock tend to make heterogeneous use of available land, due to the uneven distribution of available plants, accumulated excreta, soil and water resources, as well as topography (Vallentine, 2000). Grazing animals must forage for and select a diet from a range of available foods to meet nutrient requirements, even in monocultured, intensively managed swards (Forbes, 1995). In species-rich grasslands, animals encounter various plant species whose morphology, availability, quality and phenology differ widely.

The diet selected by herbivores and spatio-temporal differences in land use can have profound implications for nutrient intake (e.g., energy, protein and minerals), the intake of plant secondary metabolites and toxins, and changes in the botanical composition

of grasslands (Vallentine, 2000; Rook and Tallwin 2003; Ogura et al., 2006a). Research on herbivore diet selection and foraging behavior is important for livestock productivity and health and for the biodiversity and sustainability of grassland ecosystems (Fig 1). Despite extensive studies of herbivore grazing designed to deepen our understanding of diet selection in grazing cattle, the underlying mechanisms remain unclear, since so many factors affect selective grazing (Saiga, 1990; Mohammad et al., 1995; Vallentine, 2000).

This review summarizes previous findings on diet selection by grazing cattle on Japanese native grasslands and discusses various factors affecting selective grazing and foraging behavior in cattle, with reference to recent research topics.

1. Number of plant species available and consumed by cattle on Japanese native grasslands

Surveying the plant species that occur in grasslands and that contribute to the diet of cattle is a first step toward understanding diet selection in grazing cattle. Several field measurements have been carried out for different sites, vegetation, animal breeds and seasons (Table 1). The number of plant species available on grasslands ranges from 14 to 118 for each season. This variation may be attributable to the characteristics of the vegetation itself, to differences in sampling methods, or to the number and size of plots or classification of species groups (e.g., *Carex* spp. and *Asteraceae*). Of these plant species, cattle consumed from seven to 55 species, accounting for proportions ranging from 0.229 to 0.875. The researches in Japan and some recent research in Europe (Mayer et al., 2003; Dumont et al., 2007) involved plant canopy measurements (i.e., recording the frequency

of grazed/browsed plants) and observations of biting behavior in the animals observed. Microscopic observations of ingesta from esophageal fistula or fecal samples are also known to be useful (Mohammad et al., 1995; Ortega et al., 1995). The number of forage species has grown with the volume of data gathered over the seasons and years. Reviewing past studies of plant selection by cattle in Japanese native grasslands and forests, Okano and Iwamoto (1989) reported that cattle ingested 478 of 644 available plant species. Regression analysis indicates a strong relationship ($P < 0.001$) between the number of plant species in the diet of cattle and the number of plant species available (Fig. 2). The value of the slope (0.579) is the average proportion of plant species consumed by cattle in Japanese native grasslands. This linear relationship indicates that cattle consume more plant species when more species are available.

Some reports showed that plant selection among grazing cattle varies from season to season on native grasslands (e.g., Andrew, 1986; Cruz and Ganskopp, 1998; Willms and Rode, 1998). Aizawa et al. (1973) and Fukukawa et al. (1979) reported that cattle consumed a wider range of plant species in autumn than in spring or summer. Fukukawa et al. (1979) also pointed to an increase in the number of plant species consumed by cattle with higher stocking intensities, suggesting that declining forage availability in the autumn expands the number of plant species consumed by cattle.

2. Evaluation of preference of cattle for native plant species

Relative preference (RP) (Hodgson, 1979; Vallentine, 2000), and selectivity index (SI) (Jacobs, 1974; Andrew, 1986; Coates and Penning, 2000) are useful

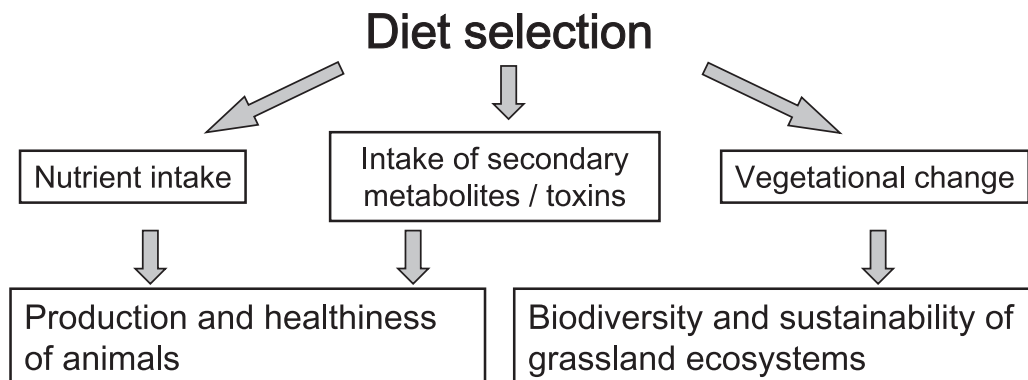


Fig. 1. Importance of diet selection of herbivore animals in grazing systems.

Table 1. A list of researches showing the number of plant species available and consumed by cattle in native grasslands.

Year	Research site	Pasture type	Dominant species	Cattle breed ¹⁾	Season	No. of species		Measurement technique used for diet estimation	Reference
						as available (A)	as consumed (B)		
1955	Miyagi, Japan	Native pasture	<i>Miscanthus sinensis</i>	JB	summer-autumn	155	76	Plant based	Iizumi et al. (1956a; 1956b)
1956	Hiroshima, Japan	Native pasture	<i>Miscanthus sinensis</i>	JB	spring	14	9	Plant based	Ito (1962)
1956	Hiroshima, Japan	Native pasture	<i>Arundinella hirta</i>	JB	spring	18	15	Plant based	Ito (1962)
1956	Hiroshima, Japan	Native pasture	<i>Zoysia japonica</i>	JB	spring	22	15	Plant based	Ito (1962)
1956	Hiroshima, Japan	Native pasture	<i>Plantago asiatica</i>	JB	spring	16	14	Plant based	Ito (1962)
1963	Miyagi, Japan	Native pasture	<i>Miscanthus sinensis</i>	JB	summer	80	44	Plant based	Sato (1996)
1969-1971	Ehime, Japan	Young tree plantation	<i>Miscanthus sinensis</i>	JB	3 years	185	103	(No information)	Utsunomiya (1973)
1974	Tochigi, Japan	Native pasture	<i>Miscanthus sinensis</i> , <i>Cymbopogon tortilis</i>	HS	autumn	39	22	Plant based	Fukukawa et al. (1979)
1975	Tochigi, Japan	Native pasture	<i>Miscanthus sinensis</i> , <i>Cymbopogon tortilis</i>	HS	autumn	36	12	Plant based	Fukukawa et al. (1979)
1972	Fukushima, Japan	Native pasture	(No information)	JB	autumn	34	13	Plant based	Fukukawa et al. (1979)
1973	Fukushima, Japan	Native pasture	(No information)	JB	autumn	26	13	Plant based	Fukukawa et al. (1979)
1974	Fukushima, Japan	Native pasture	(No information)	JB	spring	34	12	Plant based	Fukukawa et al. (1979)
1975	Fukushima, Japan	Native pasture	(No information)	JB	spring	26	12	Plant based	Fukukawa et al. (1979)
1975	Fukushima, Japan	Native pasture	(No information)	JB	autumn	36	22	Plant based	Fukukawa et al. (1979)
1973	Nagano, Japan	Native pasture	(No information)	AN	autumn	21	13	Plant based	Fukukawa et al. (1979)
1992	Miyagi, Japan	Native pasture	<i>Pteridium aquilinum</i> , <i>Miscanthus sinensis</i>	JB	summer	61	48	Plant based	Matsumoto and Sugawara (1995)
1992	Miyagi, Japan	Native pasture	<i>Pteridium aquilinum</i> , <i>Miscanthus sinensis</i>	JB	autumn	33	23	Plant based	Matsumoto and Sugawara (1995)
1996-1999	Miyazaki, Japan	Young tree plantation	<i>Miscanthus sinensis</i>	JB	4 years	176	118	Biting behavior	Hirata et al. (2008)
2002	Miyagi, Japan	Native pasture	<i>Astilbe thunbergii</i> , <i>Miscanthus sinensis</i>	JB, JS	autumn	49	23	Biting behavior	Takahashi et al. (2003)
2002	Miyagi, Japan	Native pasture	<i>Miscanthus sinensis</i> , <i>Calamagrostis arundinacea</i>	JB, JS	autumn	53	19	Biting behavior	Takahashi et al. (2003)
2003	Gifu, Japan	Native pasture	<i>Pleioblastus chino</i>	JB	spring	87	55	Biting behavior	Yayota et al. (2008)
2003	Gifu, Japan	Native pasture	<i>Pleioblastus chino</i>	JB	summer	102	51	Biting behavior	Yayota et al. (2008)
2003	Gifu, Japan	Native pasture	<i>Pleioblastus chino</i>	JB	autumn	118	55	Biting behavior	Yayota et al. (2008)
2008	Miyagi, Japan	Native pasture	<i>Arthoxanthum odoratum</i>	JB	summer	40	11	Biting behavior	Yokoyama et al. (2009a)
2008	Miyagi, Japan	Native pasture	<i>Pteridium aquilinum</i>	JB	autumn	42	10	Biting behavior	Yokoyama et al. (2009a)
2008	Miyagi, Japan	Native pasture	<i>Miscanthus sinensis</i>	JB	summer	27	7	Biting behavior	Yokoyama et al. (2009a)
2008	Miyagi, Japan	Native pasture	<i>Miscanthus sinensis</i>	JB	autumn	35	8	Biting behavior	Yokoyama et al. (2009a)
1961	California, USA	Rangeland	<i>Bromus</i> spp.	HF	summer	48	42	Faecal analysis	Van Dyne and Heady (1965)
-	-	-	-	-	-	644	478	-	Okano and Iwamoto (1989)

1) AN: Angus, HF: Hereford, HS: Holstein, JB: Japanese Black, JS: Japanese Shorthorn.

2) Including number of species and species groups. Each species group was counted as 1 species.

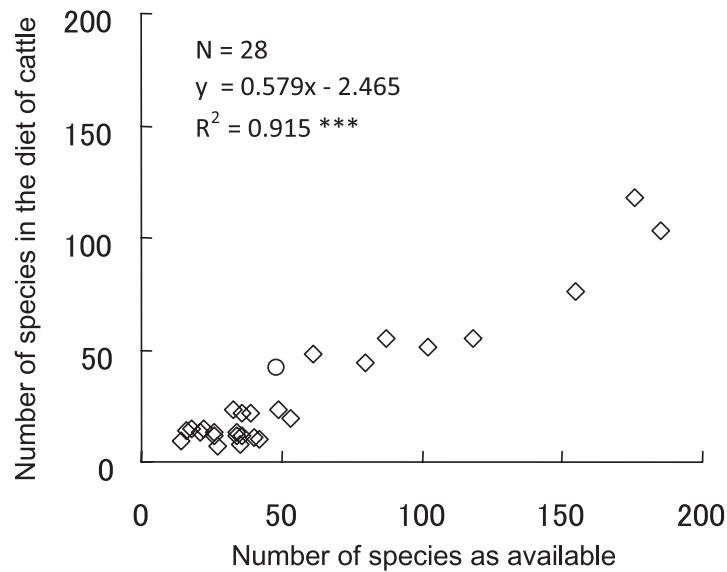


Fig. 2. Relationship between the number of plant species in the diet of cattle and as available in grasslands. The data were collected from Table 1. Diamonds and a circle represent the data from Japan and USA, respectively.

parameters for evaluating how strongly cattle prefer individual plant species. Recent studies showed the high RP of *M. sinensis* among cattle in summer and autumn, both on native grasslands in a northeastern region (Yokoyama et al., 2011) and in a young tree plantation in a southwestern region (Takahashi et al., 2000a; 2000b). The results show cattle graze intensively on *M. sinensis* during the grazing seasons, regardless of climate condition and accompanying plants species.

However, *M. sinensis* is susceptible to damage by defoliation and trampling by grazing cattle and deteriorates under conditions of high stocking intensity within several years (Takahashi et al., 2009). Clarifying why grazing cattle so strongly prefer *M. sinensis* will help improve livestock management and the conservation of native grasslands.

3. Factors affecting plant preference among cattle: chemical and behavioral approach

Grazing researchers have spent considerable time and effort investigating cognitive factors in grazing animals related to forage plants and foraging behavior. Although intake rate maximization theory has generally prevailed in explaining the foraging behavior of large herbivores (Stephens and Krebs, 1986), recent studies suggest the rate of energy intake is not the currency being optimized by the animals (WallisDeVries and Schippers, 1994; Rutter et al., 2004). Current limitations on our understanding in this area

make it difficult to extrapolate from simple models to the more complex swards that concern biodiversity managers (Rook and Tallowin, 2003).

In Japanese native grasslands, despite high preference for *M. sinensis*, previous reports point to the relatively low nutritive value of native grasses. For example, concentrations of crude protein (CP) in *M. sinensis* and *Z. japonica* are 69–74 g/kg DM and 71–102 g/kg DM, respectively, lower than for orchardgrass (*Dactylis glomerata*) (156–171 g/kg DM) growing in the same pasture (Ogura et al., 2001). Hirata et al. (2008) also showed lower dry matter digestibility (DMD; 399–528 g/kg DM) and CP (134–208 g/kg DM) for *M. sinensis* than in the diet of cattle grazing on other species (DMD; 427–587 g/kg DM, CP; 70–150 g/kg DM), due to the higher quality of the major forbs and woody plants consumed by the latter cattle. Takahashi et al. (2006) report on the absence of any significant relationship between intake rates and CP concentrations. Yokoyama et al. (2009b) report that TDN, CP, and minerals failed to explain the RP for native plants. One possible explanation is that toxic plants (*Hydrangea macrophylla* and *Pteridium aquilinum*) have high nutrient concentrations (Yokoyama et al., 2009b).

It is necessary for herbivores to obtain and process information on their foraging choices in a way that maximizes nutritional intake rate and minimizes the risk posed by toxic substances. Several channels are involved in processing this information, including

temporally distinct perspective faculties such as sight and smell, which precede consumption, and retrospective faculties such as touch, taste, gut distention, and nutrient absorption (Illius and Gordon, 1993) (Fig. 3). Botanical and behavioral factors corresponding to these faculties affect the food choice of herbivores in each channel.

3-1. Chemical components affecting diet selection

Saiga (1990) concluded that cattle prefer species with broader leaves, less fiber, fewer toxic substances, more sugar, and higher digestibility. Reviewing the chemical compounds that stimulate the senses of taste and smell, Dohi (1996) classified the chemical components perceived by herbivores as sweet, savory, salty, sour, bitter, or astringent, as gustatory receptors in large herbivores are similar to those in humans. Reports also suggest that the taste sense of livestock is a major factor in the apparent palatability of perennial ryegrass (*Lolium perenne*) (Dohi et al., 1996; 1997b). These studies of gustatory stimuli have been applied to plant breeding. For example, Mayland et al. (2000) reported that concentrations of total soluble sugar correlate with a preference for tall fescue (*Festuca arundinacea*) cultivars. However, information is scarce on the concentrations of chemical components

that increase palatability (e.g., soluble sugars and amino acids) in native plants, while a partial finding was reported on the concentration of amino acids and soluble oligosaccharides in *Zoysia species* (Akiyama et al., 1994).

In contrast to gustatory substances, flavor components are less easily classified into the fundamental elements of stimuli like tastes, due to the great variety of perceptions present in olfactory sensations (Dohi, 1996). In addition, the combination of two or more flavor components may result in quite different effects when combined with different olfactory stimuli. Due to the intricacy of the relationship between olfactory sensations and plant flavor components, the chemical components in plants that stimulate olfactory sensation of herbivores have yet to be identified. Thus, most studies have analyzed the volatile components found in foodstuffs (Dohi, 1996).

Researchers have also examined the relationship between leaf surface volatiles found on herbage plants and the corresponding palatability for livestock. Scehovic (1985) reported that volatile compounds reduced the palatability of tall fescue. Dohi et al. (1997a) reported that the presence of cis-3-Hexenol inhibited feeding among goats. Recent research analyzing volatile flavor compounds from samples of the headspace of leaves from four native plants in-

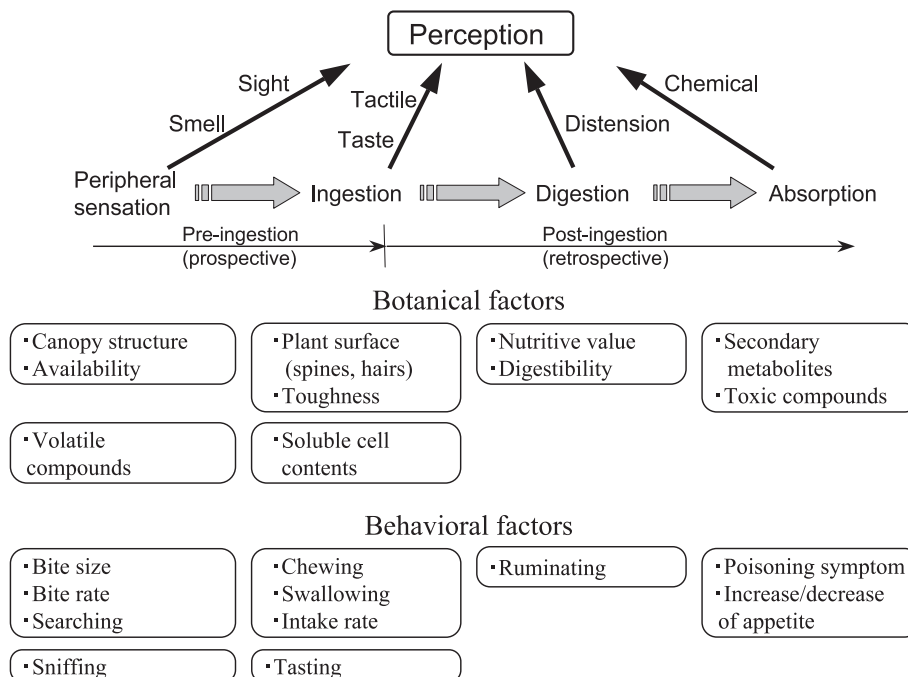


Fig. 3. Flow diagram of the processing of food and information (Illius and Gordon, 1993), and botanical and behavioral elements concerning to each channel of food perception.

dicated that some are unique to certain plant species (Yokoyama et al., 2011). These findings suggest that cattle can use the volatile compounds in association with other plant characteristics, such as the tactile and taste characteristics, as cues for identifying particular plant species.

3-2. Behavioral factors

Behavioral factors interact with the faculties that affect grazing behavior (Fig. 3). Bite size constitutes the smallest and shortest observable component of foraging behavior in space and time, respectively (Senft, 1987; Coleman et al., 1989; Bailey et al., 1996). Takahashi et al. (2006) quantified bite size, bite rate and dry matter intake rate for cattle in a *Miscanthus*-dominated native pasture, suggesting that intake rate of DM and CP could be reduced as cattle took more bites *M. sinensis* due to its smaller bite size. A recent study showed that RP was significantly explained to predicted bite size of beef cattle (Yokoyama et al., 2009a).

Takahashi et al. (2007) examined the relationships between frequency of bites taken by beef cattle and the canopy structure of native plants, focusing on the vertical distribution of biting behavior and plant parts. Their results showed that cows took more bites from layers with more available leaves. For example, for *M. sinensis*, a significant portion of the leaves during summer were found within a height of 40–60 cm, and a high proportion of the bites was distributed within this range of heights. Correlation analysis showed a positive relationship between the proportion of bites and available leaf mass. These results suggest that the distribution of available forage is a major factor of diet selection and foraging behavior in cattle. Ogura et al. (2006b) performed a feeding trial to determine if the height of the available forage affected preference and intake rates for cattle, constructing a structure and setting out equal amounts of hay at different heights. With the hay set at four different heights, cows took more from 70 cm and 120 cm than from the height of 20 cm and 170 cm. The highest intake rate was observed for 70 cm when hay was set at one of the four heights. These findings strongly suggest that vertical height affects food selection and foraging behavior among herbivores. The height of 70 cm is nearly identical to the height at which the leaves of *M. sinensis* abundantly occur (Takahashi et al., 2007). The characteristics of the canopy structure of

Miscanthus-dominated pastures may offer beneficial foraging conditions that allow cattle to ingest forage plants at higher intake rates.

4. Implications: function of grazing in the species-rich grasslands

This study examined the selection of native plants as forage by cattle and factors affecting such selection on Japanese native grasslands. Among various chemical and behavioral factors, bite size is a parameter significantly related to RP for native plant species, possibly more so than chemical factors. The distribution of available leaves also proved to be an important factor affecting preference and foraging behavior. These findings help explain why cattle prefer *M. sinensis* and certain other major plants species and should help predict both voluntary intake among herbivores and vegetational change in *Miscanthus*-dominated pastures. However, earlier studies showed that chemical substances derived from native plants could also affect diet selection and foraging behavior. More study is needed to clarify the mechanisms underlying the chemical-behavioral response complex leading to diet selection.

In the next phase of our research, more work will be done to explore the following two questions: Why do grazing herbivores consume such a wide range of plant species? What role does diet selection of herbivores play in the grassland ecosystem? This future study should help advance plant species conservation in native pastures and contribute to productivity gains for grazing livestock.

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