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Intake patterns of sheep offered nutritious alternatives associated with plant secondary compounds

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SUMMARY – In grazing systems, ruminants can choose among plants with different nutritive value and different kinds and levels of plant secondary compounds (PSCs). In turn, their foraging decisions influence plant diversity. We investigated patterns of food intake by sheep fed two familiar nutritious diets (alfalfa and alfalfa-barley mixture) and three high-quality diets, each containing different PSCs (oxalates, tannins, and terpenes). The experiment consisted of two consecutive 8 day periods: conditioning and testing. During conditioning, the three PSC-containing diets were offered *ad libitum* while the two familiar nutritious foods were restricted to 300 g/d; during testing all five diets were offered *ad libitum.* In both periods, sheep were fed from 08:00 to 16:00 during which all diets were simultaneously offered to sheep and their intakes were recorded. During conditioning, consumption of all three PSCs increased (P≤0.001). Intake of the alfalfa-barley diet was the highest (984 g/d) during testing when sheep consumed more of the diet that contained tannin (471 g/d) than oxalate (181 g/d) or terpene (180 g/d). Intake of all diets across days was higher during the first hour than during the remaining hours (P≤0.001). These data suggest: (i) there may be several equally successful ways for animals to select their diets, particularly when more than two complementary diets are available; (ii) food intake increases when animals eat diets containing complementary PSCs; (iii) animals learned the benefits of such complementarities; and (iv) they continued to consume PSC-containing diets even when they had *ad libitum* access to other nutritious diets. This implies that grazing management can influence the foraging behaviour of animals by influencing the availability of alternative diets.

Key words: Diet selection, grazing, oxalates, tannins, terpenes.

RESUME – *"Tendances de l'ingestion chez des ovins recevant différentes options alimentaires liées aux composés végétaux secondaires". Dans les systèmes de pâturage, les ruminants peuvent choisir parmi des plantes ayant différentes valeurs nutritives et différents types et niveaux de composés végétaux secondaires (PSC). En retour, leurs décisions concernant l'herbe qu'ils broutent influencent la diversité végétale. Nous avons étudié les tendances de l'ingestion alimentaire par des ovins recevant deux régimes alimentaires ordinaires (luzerne et mélange luzerne-orge) et trois régimes de haute qualité, contenant chacun différents PSC (oxalates, tannins, et terpènes). L'expérience a consisté en deux périodes consécutives de 8 jours : adaptation et test. Durant l'adaptation, les trois régimes contenant des PSC furent offerts* ad libitum *tandis que les deux aliments ordinaires furent restreints à 300 g/j ; durant le test les cinq régimes furent offerts* ad libitum*. Pendant les deux périodes, les ovins étaient alimentés de 08:00 h à 16:00 h, tous les régimes étant offerts de façon simultanée aux ovins en enregistrant leur ingestion. Pendant l'adaptation, la consommation des trois PSC augmenta (P≤0,001). L'ingestion du régime luzerne-orge était la plus élevée (984 g/j) pendant le test lorsque les ovins consommaient davantage d'aliment contenant des tannins (471 g/j) que des oxalates (181 g/j) ou des terpènes (180 g/j). L'ingestion de tous les régimes sur ces journées était plus élevée pendant la première heure que pendant les heures restantes (P≤0,001). Ces données suggèrent que : (i) il peut exister pour les animaux plusieurs façons également performantes de sélectionner leur alimentation, en particulier lorsque plus de deux régimes complémentaires sont disponibles ; (ii) l'ingestion alimentaire augmente lorsque les animaux consomment des régimes contenant des PSC complémentaires ; (iii) les animaux ont appris les bénéfices de ces complémentarités ; et (iv) ils continuent de consommer des régimes contenant des PSC même lorsqu'ils peuvent accéder* ad libitum *à d'autres aliments. Ceci implique que la gestion du pâturage peut influencer le comportement de broutage des animaux en intervenant sur la disponibilité d'alimentations alternatives.*

Mots-clés : *Sélection de l'alimentation, pâturage, oxalates, tannins, terpènes.*

Introduction

Herbivores foraging on diverse plant communities can choose from a wide array of chemicals –

different nutrients and plant secondary compounds (PSCs) – that create a multidimensional grazing environment. Herbivores modify vegetation by selecting diets composed of several plants and by sampling available plants on a regular basis. Thus, plant biochemical variability and selective grazing by animals affect the structure and diversity of plant communities (Provenza *et al*., 2003).

The process of diet selection is influenced by complex interactions among nutrients, PSCs and animal experience (Provenza, 1995, 1996; Hanley, 1997; Villalba *et al*., 2004). Nutrients and PSCs both influence the kinds and amounts of forages ingested as animals attempt to meet their nutritional needs (Westoby, 1978) and regulate intake of PSCs (Freeland and Janzen, 1974). Moreover, interactions among these plant chemicals can lead to complementary relationships among forages because eating a combination of diets may exceed the average benefit of consuming the diets in isolation (Tilman, 1982; Villalba *et al*., 2004). Nutritional state also influences how much PSCs animals can ingest. By facilitating detoxification processes, supplemental energy and protein increase the ability of animals to eat diets that contain either toxins or PSCs (e.g. lithium chloride, menthol, terpenes, tannins and saponins; see Provenza *et al*., 2003). Thus, supplemental nutrients help animals cope with plants containing PSCs and reduce the time they require to adapt to feeding on such plants.

Experiences of both the social and physical environments shape behaviour, which influences gene expression (McCormick *et al*., 2000; Duffy *et al*., 2002), and improves performance by inducing neurological, morphological, and physiological changes in animals (Provenza, 1995, 1996). Such flexibility enables adaptation to different grazing conditions and implies that learning influences responses of animals to diets and habitats (Davis and Stamps, 2004). In this study, we hypothesised that if animals have been trained to eat PSC-containing diets under the right nutritional context (i.e. adequate kinds and amounts of nutrients), they should eat those diets even when nutritious alternatives are available.

Materials and methods

The study was conducted at the Utah State University Green Canyon Ecology Center, in Logan, Utah during August 2004. Five diets were used: two nutritious alternatives (alfalfa and alfalfa-barley 50:50) and three nutritious diets containing PSCs. The three PSC-containing diets were isoenergetic (DE: 2.9 Mcal/kg; NRC, 1985) and isonitrogenous (CP: 126 g/kg; NRC, 1985) and they were formulated using the same ingredients: (i) oxalate-containing diet (67.5% ground beet pulp, 20% ground grape pomace, 11% soybean meal and 1.5% oxalic acid); (ii) tannin-containing diet (76% ground beet pulp, 9% soybean meal and 15% quebracho tannin); and (iii) terpene-containing diet (52.8% ground beet pulp, 26% ground grape pomace, 14% soybean meal, 1.82% camphor, 1.1% 1-8-cineole, 0.12% methacrolein, 0.06% p-cymene and 4.1% vegetable oil). Twelve male and female commercial crossbred lambs, 5 to 6 months old, were used. They were naive to the three PSC-containing diets but they had experience with eating alfalfa and alfalfa-barley. Sheep had a mean live weight of 47 kg (SD = 1.4) kg. They were individually penned with free access to trace mineral salt blocks and fresh water.

The study consisted of: (i) a familiarization period; (ii) a conditioning period designed to give a group of 12 sheep experience with the three PSC-containing diets; and (iii) a testing period. During the 9 days of familiarization, animals were fed all the ingredients of the PSC-containing diets without the PSCs. On day 9, sheep consumed more or less 300 g/d of each of the PSC-containing diets. During conditioning, the three PSC-containing diets were offered *ad libitum*, but the two familiar nutritious diets were restricted to 300 g/d. During testing, all five diets were offered *ad libitum.* Both conditioning and testing periods lasted 8 d. On each day, all diets were offered simultaneously to sheep from 08:00 to 16:00 h. During conditioning intake of each diet was recorded at 16:00 h while during testing food intake was recorded hourly.

Data from conditioning and testing were analysed separately using analysis of variance. Animals were blocks in the conditioning and diet was the whole-plot effect. Day, and its interaction with treatment, was a sub-plot in the analysis, and it was treated as a repeated measure. In the testing, animal, time and diet were used as block effects with time nested within diet and diet nested within animal to account for the repeated measures. Day, diet, time and their interaction were used as treatment effects.

Results and discussion

Conditioning

Intake of the PSC-containing diets during conditioning increased for animals for all three PSCs (P≤0.001; Fig. 1). Intake rose from 18 g (1st day) to 441 g (8th day) for the terpene diet, from 176 g to 551 g for the tannin diet, and from 261 g to 483 g for the oxalate diet. The average intake of the tannin-containing diet (482 ± 56 g) by sheep across the 8-day period was higher (P≤0.05) than intake of the oxalate-containing diet (438 ± 32 g), and that was higher than the terpene-containing diet (302 ± 55 g) (P≤0.05). Sheep consumed all of the alfalfa and alfalfa-barley mix, both of which were offered in restriction. The total intake of the three PSC-containing diets in the last 4 d of conditioning ranged from 1424 to 1475 g. This provides evidence that the lack of alternatives helps animals learn to use different kinds of PSCs thereby enhancing diet breadth, which depends on prior foraging experience and nutrient-PSC interactions (Villalba *et al*., 2004).

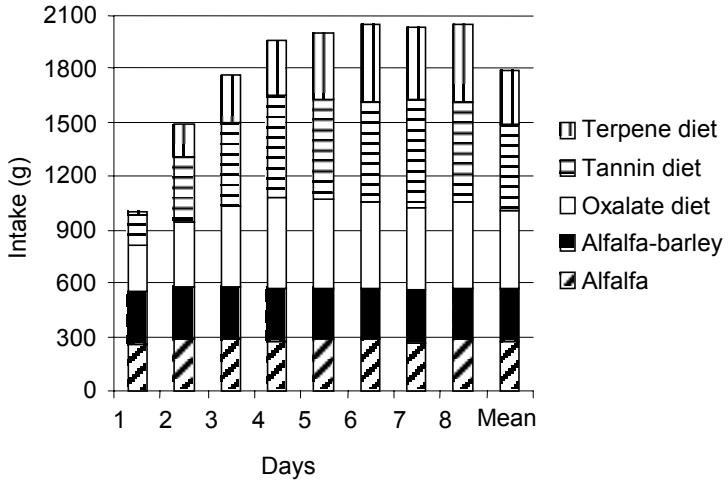

Fig. 1. Intake by sheep of diets containing oxalates, tannins, or terpenes during 8-d conditioning period when both nutritious alternatives, alfalfa and alfalfa-barley, were offered in restriction (300 g/sheep/d for each diet). Diet and diet × day means separated by more than 26 and 74 g, respectively differ ($LSD_{0.05}$).

Testing period

Intake of the alfalfa-barley diet was the highest (984 g/d) during testing when all diets were offered simultaneously *ad libitum* (P≤0.001; Table 1). Sheep consumed more of the tannin-containing diet (471 g/d) and alfalfa (440 g/d) than the oxalate-containing diet (181 g/d) or the terpene-containing diet (180 g/d). In a previous study, sheep that learned to eat diets containing tannins, terpenes, and oxalates ate more when they were offered any two of the diets (tannins-terpenes, tannins-oxalates or terpenes-oxalates) than when diets were offered individually (Villalba *et al*., 2004). Thus, the three PSC-containing diets used in the present study are complementary.

Sheep offered diets containing all three PSCs ate on average 832 g/d from diets containing PSCs, which was less than for the two nutritious alternatives (1423 g/d). However, it has been reported that sheep offered diets containing these PSCs had intakes similar to sheep offered the same diets without PSCs (Villalba *et al*., 2004). This indicates that the kinds of alternatives affect the amount of PSCs consumed by animals. In that study and the study reported here, animals learned to mix PSC-containing diets with nutritious alternatives when they were experienced and both nutritious alternatives and PSC-containing diets were concurrently offered *ad libitum*.

Table 1. Hourly intake (g) by sheep of two nutritious diets (alfalfa and alfalfa-barley) and three plant secondary compound-containing diets (oxalates, tannins and terpenes) during testing. All diets were offered to sheep *ad libitum* for eight days from 08:00 to 16:00 h

Diet	Hour								Total/d
	09:00	10:00	11:00	12:00	13:00	14:00	15:00	16:00	
Alfalfa	138	55	41	36	41	41	44	45	440
Alfalfa-barley	333	101	84	66	63	107	112	118	984
Oxalate-	56	29	19	20	13	14	18	13	181
Tannin-	165	61	33	36	37	48	46	46	471
Terpene-	27	9	16	16	34	20	43	16	180
Total/h	718	254	193	174	188	230	263	237	2256
Significance of		SED							
Diet	***	70							
Hour	***	17							
Interaction	***	11							

***: P≤0.001.

Sheep ingested significantly more of all tested diets from 08:00 to 09:00 compared to the remaining hourly intervals (Table 1). The total daily intake was 2256 g and 1/3 of it was ingested the first hour. There was significant variation among individuals when offered the three PSC-containing diets (Fig. 2). Food intake and preference depend on differences in how individual animals are reared and acquired morphological and physiological characteristics, and even closely related animals express differences in the need for nutrients and ability to cope with PSCs (Provenza *et al*., 2003).

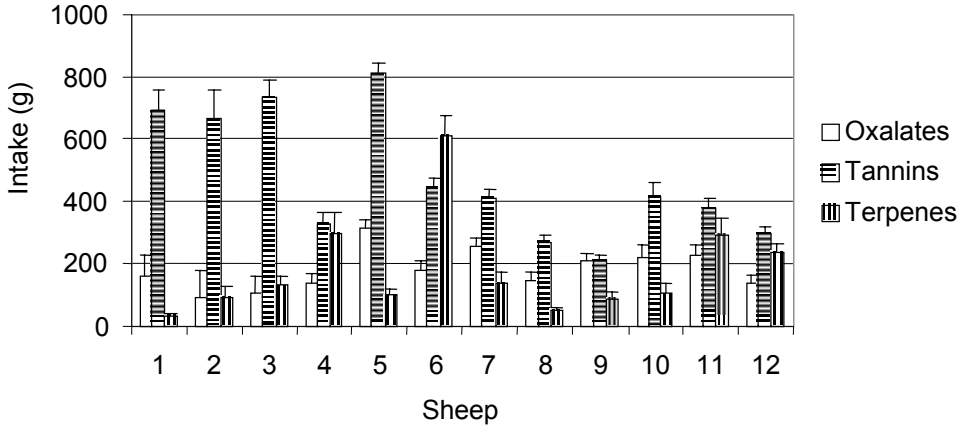

Fig. 2. Variation among 12 sheep in intake of diet that contained one of three plant secondary compounds – oxalates, tannins or terpenes. Bars are standard errors of means (n = 8 days).

In general, forcing animals to ingest complementary diets containing PSCs leads to an increased intake of those diets across time (Villalba *et al*., 2004). Beyond this effect due to diet restriction (e.g. an equivalent in nature is animal aggregation), animals learned the benefits of such complementarities and continued to consume PSC-containing diets even when they subsequently had *ad libitum* access to safe nutritious diets. Also, Fig. 2 suggests there may be several equally successful ways by which animals build their diets, particularly when more than 2 complementary resources are available and thus several complementary associations are possible as a function of the amount of each ingredient consumed.

Conclusions and implications

Learning to mix diets that differ in kinds and concentrations of nutrients and PSCs can enhance diet breadth and promote a more uniform use of all plants in a community, which in turn may influence the structure and function of ecosystems. Conversely, lack of experience and/or inadequate training of animals may diminish diet breadth and result in less uniform use of plants in a community. This study shows that different foraging strategies are possible when animals have even as few as five choices. The availability of nutritious alternatives, as well as the type of PSCs influenced patterns of diet mixing. With restriction of nutritious alternatives, sheep learned complementarities among nutritious and PSC-containing diets. This foraging behaviour continued when experienced sheep were offered nutritious-safe and PSC-containing diets in unrestricted availability. These findings suggest that grazing management can influence the foraging behaviour of animals by influencing the availability of alternatives.

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