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Patterns of diet mixing by sheep offered foods varying in nutrients and plant secondary compounds

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Abstract

Ruminants foraging on landscapes choose among plants that differ in nutritive value and kinds and amounts of plant secondary compounds (PSCs). We hypothesized that food availability and the sequence of food ingestion influence intake of PSCs and nutritious foods by sheep because PSCs increase need for nutrients. We fed two nutritious foods – alfalfa and alfalfa–barley mixture (50:50) – and three isoenergetic (DE: 2.9 Mcal/kg) and isonitrogenous (CP: 126 g/kg) foods that contained oxalates, tannins, or terpenes. The experiment consisted of an 8-d conditioning period and four trials in which we tested our hypotheses. In the conditioning period, the three PSC-containing foods were offered *ad libitum* but the two nutritious foods were restricted to 300 g/d and the daily intake of each food was measured. In trial 1, all five foods were offered from 0800 to 1600 h. In trial 2, the two nutritious foods were offered from 0800 to 1200 h whereas the three PSC-containing foods were offered from 1200 to 1600 h. In trial 3, the three PSC-containing foods were offered from 0800 to 1200 h while the two nutritious foods were offered for the next 4 h. Finally, in trial 4 all five foods were offered again from 0800 to 1600 h. Each trial lasted 8 d, except the last one, which was 5 d. In the four trials, foods were offered *ad libitum* and the amount of each food ingested was measured daily at hourly intervals. As conditioning progressed, consumption of all three PSC-containing foods increased, and the pattern of eating changed from oxalate > tannin > terpene to tannins > oxalates > terpenes. During trial 1, lambs ate alfalfa–barley > alfalfa = tannins > oxalates = terpenes. In trial 2, sheep ate 1490 g/d of nutritious foods in the morning and 863 g/d of PSC-containing foods in the afternoon for a total of 2353 g/d. In trial 3, when the sequence was reversed, sheep ate 1021 g/d of PSC-containing foods in the morning and 1564 g/d of the nutritious foods in the afternoon for a total of 2585 g/d. By trial 4, the

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pattern of diet mixing had changed such that sheep ate alfalfa–barley > tannins > alfalfa = terpenes > oxalates. In summary, sheep ate more PSC, and more nutritious food, when PSCs were offered in the morning as opposed to the afternoon. Limiting the availability of nutritious alternatives encouraged animals to learn to use different kinds of PSCs and enhanced diet breadth. Beyond the effect of diet restriction, lambs learned the benefits of mixing food with tannins, terpenes, and oxalates and continued to do so even when they subsequently had *ad libitum* access to nutritious foods.

Keywords: Diet selection; Grazing; Landscape biodiversity; Oxalates; Plant–herbivore interactions; Tannins; Terpenes

1. Introduction

Herbivores foraging in diverse plant communities encounter a wide array of biochemicals – different nutrients and plant secondary compounds (PSCs) – that create a multidimensional feeding environment (Bryant et al., 1991). Interactions among these chemicals can lead to complementary relationships among foods when eating a combination of foods exceeds the benefit of consuming the foods in isolation (Tilman, 1982; Villalba et al., 2006). For instance, lambs that choose a combination of foods that contain compounds such as amygdalin, lithium chloride, nitrates, oxalates, tannins and terpenoids eat more than lambs offered a single food that contains only one of these compounds (Burritt and Provenza, 2000; Villalba et al., 2004). In addition, by facilitating detoxification processes, supplemental nutrients – energy and protein – increase the ability of animals to eat foods that contain compounds as diverse as lithium chloride, menthol, terpenes, tannins, and saponins (Provenza et al., 2003). Conversely, restricting the availability of nutrients such as sodium in the diet limits the amount of toxins an animal can ingest, and the sodium-depleting effects of many toxins may deter herbivores from eating plants with PSCs when eating diets low in sodium (Freeland et al., 1985; Freeland and Choquenot, 1990). Thus, supplemental nutrients help animals cope with PSCs, influence preferences for foods high in PSCs, and likely reduce the time animals require to adapt to PSCs.

Experience and the availability of nutritious alternatives influence the ability of animals to learn to mix foods that differ in kinds and concentrations of nutrients and toxins. Animals can learn to eat complementary mixtures of foods that contain nutrients and PSCs. For instance, lambs with experience eating foods high in tannins, terpenes, and oxalates eat more of those foods than naïve animals even when nutritious foods are available *ad libitum* to both groups (Villalba et al., 2004). Learning to mix foods that differ in kinds and concentrations of nutrients and PSCs can enhance diet breadth and promote more uniform use of all plants in a landscape, which can influence the structure and function of ecosystems (Provenza et al., 2003). Importantly, the sequence of food ingestion may influence how herbivores learn about PSCs and how much PSCs they can ingest each day. For instance, herders in France move sheep and goats in daily grazing circuits designed to enhance intake and use of diverse forages (Hubert, 1993; Meuret et al., 1994). Unfortunately, we know little about how the sequence in which nutrients and PSCs are ingested affects intake.

We hypothesized that food availability and the sequence in which foods are eaten during the day both influence intake and preference for PSCs and nutritious foods because PSCs increase need for nutrients. Based on this hypothesis, we predicted (1) sheep offered PSCs in the morning and nutritious foods in the afternoon would eat more foods with PSCs and more nutritious foods than sheep offered nutritious foods in the morning and PSCs in the afternoon, and (2) given the appropriate experience with a nutrient/PSC context, they would continue to eat such foods even