Toxins Reduce Palatability

Several years ago we had two research projects we assumed were unrelated. One focused on why goats avoid the current season's growth of blackbrush and the other on how livestock learn to avoid foods high in toxins. We proposed that tannins caused goats to avoid current season's growth. We believed that herbivores "innately" dislike the flavor of tannins because tannins are astringent and taste bad. On the first day of our feeding trial, goats readily ate both plain pellets and tannin-coated pellets. But on the next day, they switched to eating only plain pellets. As we thought about these results we realized blackbrush tannins are toxic, toxins cause food aversions (illness), and goats learn very quickly to avoid current season's growth. On that day, we also began to realize that our projects were not unrelated. The experiment changed how we view palatability and diet selection. We began to wonder, how many other unpalatable plants might contain toxins that cause food aversions?

Toxins are everywhere. It turns out all plants contain toxins, even common vegetables, so herbivores can't avoid ingesting toxins. Few toxins are ingested in amounts large enough to cause poisoning or death because animals regulate their intake depending on the concentration of the toxin in the plant. Ingesting plants with toxins is a matter of regulating rather than avoiding.

Toxins benefit plants because plants that quickly induce satiety in foragers are more likely to survive that those that do not. When toxins occur in moderate concentrations they cause herbivores to limit intake of plants thereby spreading grazing pressure more evenly across plant communities. High concentrations of toxins in some plants, such as sagebrush, severely restrict intake. Over time these plants tend to dominate rangelands, grazing gives them a competitive advantage because herbivores prefer to eat other plants lower in toxins.

Regulating intake of toxins. Animals can regulate intake of plants that contain toxins because toxins have aversive effects on the body that feed back to the palate through various nerves. That feedback causes animals to satiate, or stop eating one food and begin eating others. Thus, toxins in most plants simply limit intake but do not cause obvious signs of poisoning in herbivores. This limit on intake, called the toxin-satiation threshold, causes herbivores to eat limited amounts of many plants.

The rate at which toxins are ingested depends on how quickly they can be eliminated from the body. At high concentrations, most toxins make plants unpalatable, especially if the plant is low in nutrients. However, for plants such as larkspur that are high in nutrients relative to toxins, intake tends to be cyclical. Herbivores gradually increase intake of a nutritious toxic plant over several days. When intake exceeds the toxin-satiation threshold, preference declines for a few days, then gradually increases because of the positive postingestive consequences herbivores experience from plant nutrients. Low levels of toxins in highly nutritious plants also cause herbivores to limit intake of plants. For example, sheep grazing a clover-grass pasture prefer to eat clover in the morning and grass in the afternoon even though clover is higher in energy and protein than grass. Sheep may switch from clover to grass in part because white clover contains cyanide, a toxin that can cause food aversions in herbivores.

Eating toxins is expensive. Toxins affect the nutrient status of the body in several ways: 1) They limit food (nutrient) intake. 2) Some toxins reduce the digestibility of nutrients. 3) Once ingested, additional nutrients are required by the body to excrete the toxins.

It is difficult to determine the cost of excreting toxins because in many cases detoxification pathways are unknown. Where these pathways are known, the costs of detoxification are substantial. Most toxins are lipophilic compounds (fat loving) that must be transformed into hydrophilic substances (water loving) before they can be eliminated from the body. This conversion requires additional energy and protein. Furthermore, excretion of these compounds may disrupt the body's acid/base balance forcing the body to use additional protein and energy.

Toxin-toxin interactions. Different kinds and amounts of toxins in plants influences how much an animal can eat during a meal. Some toxins are complementary while others are antagonistic. Different toxins affect different metabolic pathways and are likely detoxified by separate pathways.

Herbivores eat more forage when the plants in their diet contain complementary toxins than when they eat a single plant with one toxin. For example, lambs fed a single diet containing either oxalate, tannin or terpenes ate less than lambs fed a choice of all three diets. Mule deer also ate less when they were fed either sagebrush or juniper than when they were offered both sagebrush and juniper, plants that contain different terpenes. In Australia, brushtail possums consumed more food when they ate two diets, one containing phenolics and the other terpenes, than possums that ate a diet containing only one of these toxins. Finally, in Texas sheep ate more when they were able to mix oak brush (tannins) and four wing saltbush (saponins) rather than either plant alone.

Conversely, herbivores cannot increase their intake of toxic foods when toxins are antagonistic. For example, lambs offered two foods, one containing the alkaloid sparteine and the other containing saponins, did not eat more total food when compared with lambs offered one food containing either saponin or sparteine.

Implications. Grazing practices such as short duration, high intensity grazing that enhance and maintain a diversity of plant species on rangelands increase the likelihood that herbivores will not over-ingest toxins. Range sites in good condition provide herbivores with a variety of species with varying levels of nutrients and toxins. These sites supply herbivores with the nutrients they need to eat and detoxify plants containing toxins providing more even use of all plant species.

On the other hand, range sites in poor condition offer herbivores limited numbers of plant species many of which contain high levels of toxins. Herbivores on these sites will likely overuse palatable plants and avoid toxic plants because they do not have adequate nutrients for detoxification. Over time these sites become dominated by a few species high in toxins.

Herbivores also benefit from grazing pastures that contain mixtures of plants that enable them to eat a variety of foods that contain different kinds and amounts of toxins. Planting pastures that prevent over-ingestion of toxins may be difficult as little is known about most toxin-toxin interactions, and people assume incorrectly that most grasses and many forbs do not contain toxic compounds. Until researchers identify the toxins in plants and determine how they affect intake, it will be hard to know exactly which species complement each other. However, planting or maintaining any mixture of plants increases the odds herbivores will be able to avoid over-ingesting any one toxin and meet nutritional needs.

References:

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