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Self-regulation of intake of polyethylene glycol by sheep fed diets varying in tannin concentrations[1]

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ABSTRACT: Tannins occur in many plant species, and they often suppress intake by reducing nutrient availability or by causing malaise. Polyethylene glycol (PEG) binds to tannins and may thereby increase the availability of macronutrients and decrease malaise. Supplemental PEG increases intake of tannin-containing plants by sheep, goats, and cattle. Given the strong response to supplemental PEG, we speculated that animals might self-regulate their intake of PEG when offered foods high in tannins. The objective of the first experiment was to determine if the amount of supplemental PEG (0, 25, 50, 75, or 100 g; molecular weight, 3,350) affected intake by lambs of a food (milo-tannin mix) containing 20% quebracho tannin. There was a linear relationship ($Y = 272 + 1.2X$; $R^2 = .86$; $P = .023$) between the amount of supplemental PEG ingested and the subsequent intake of milo-tannin food by lambs. The objective of the second experiment was to determine whether lambs self-regulated intake of PEG when fed a ration that contained 0, 5, 10, 15, or 20% quebracho tannin and whether they adjusted their intake of PEG when tannin was removed from the diet. There was a positive relationship between the amount of PEG ingested and intake of food and tannin ($P = .0001$). Lambs fed high-tannin diets ate more PEG than controls ($P = .03$). Lambs fed the 20% tannin diet ate the most PEG, and controls ate the least PEG. Tannin limited intake of the diets, but PEG attenuated the response to a great degree ($P = .065$). Immediately after tannin was removed from the ration, lambs that formerly had been fed the 20% tannin ration ate more PEG than lambs fed the other rations ($P = .0075$). Ten of the lambs (5 from the 20% tannin group, 1 from the 15% tannin, and 2 each from the 10 and 5% groups) continued to eat PEG for 7 d after tannin was removed from their ration. When they were tested again 6 wk after the trial and offered tannin-free diets, their intake of PEG had decreased.

Key Words: Intake, Polyethylene Glycol, Sheep, Tannins

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Introduction

Tannins occur in many plant species, and they often suppress food intake by reducing digestibility or by causing illness. Tannins bind to cell walls and cell solubles (Kumar and Vaithiyanathan, 1990; Reed, 1995) and, in the process, reduce the digestion of protein and the production of energy-rich by-products of microbial fermentation, such as volatile fatty acids (Robbins et al., 1987; Makkar et al., 1995). Lack of nutrients, in turn, adversely affects preference (Villalba and Provenza, 1996, 1997a,b,c, 1999). Tannins also produce aversive effects that cannot be accounted for by digestion inhibition, primarily due to such rapid (within 1 h) and dramatic decreases in food intake (Provenza et al., 1994). They are best accounted for by lesions of gut mucosa and toxicity (Kumar and Singh, 1984; Reed, 1995), which are likely to stimulate emetic mechanisms in the nervous system (Provenza et al., 1990, 1994).

Polyethylene glycol (**PEG**) binds to tannins and may thereby increase the availability of macronutrients. Supplemental PEG increases intake of tannin-containing plants by animals as diverse as rats (Horigome et al., 1988), sheep and goats (Pritchard et al., 1988; Titus et al., 1999a,b), and cattle (Hannigan and McNeill, 1998). Given the strong response to supplemental PEG, we speculated that animals might self-regulate their intake of PEG when offered foods high in tannins. Animals can learn to consume foods and solutions that attenuate aversive effects of food ingestion. Lambs ingest more sodium bicarbonate (in water or food) when eating high-grain diets, and they eat more grain when offered sodium bicarbonate (Phy and

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Provenza, 1998a,b). However, lambs prefer plain water to water with sodium bicarbonate, unless they are eating grain. Thus, lambs drink the sodium bicarbonate solution for its benefits (i.e., attenuation of malaise caused by acidosis; Provenza et al., 1994), not necessarily because they like the flavor.

We conducted two trials. The objective of the first trial was to determine if the amount of supplemental PEG affected intake of a food containing 20% tannin by lambs. The objective of the second study was to determine if lambs would voluntarily consume PEG when fed a high-tannin ration and decrease their intake of PEG when tannin was removed from their diet.

Materials and Methods

Dose of PEG

The objective of this trial was to determine if the amount of supplemental PEG affected intake by lambs of a diet containing 20% tannin. We used 6-mo-old lambs (commercial crossbreds) naive to quebracho tannin and polyethylene glycol (PEG). Lambs were weaned at 60 d and reared on alfalfa pellets, soybean meal, beet pulp, and barley. Prior to the trials, they were stratified by weight, randomly allocated to five treatments (0, 25, 50, 75, or 100 g PEG/d), and placed in individual pens. There were seven lambs per treatment. Each morning at 0800, lambs were fed 50 g of barley mixed with the appropriate amount of PEG (molecular weight, 3,350; Spectrum Chemical, Los Angeles, CA) for 15 min. Lambs ate all of their PEG-grain mixture throughout the trial. Polyethylene glycol is a white, granular substance with little odor or taste to humans; the PEG-grain mixture was offered in plastic containers. Immediately after eating the PEG-grain mixture, lambs were fed the milo-tannin mixture for 1 h. On d 1 of the trial, lambs were offered 200 g of milo-tannin, and the amount of milo-tannin offered was increased 50 g/lamb/d for 10 d. On the last day of the trial, lambs received 650 g of milo-tannin. Following daily trials, lambs were offered alfalfa pellets ad libitum until 1700. Lambs had free access to fresh water and trace-mineralized salt blocks throughout the trial.

Self-Regulation of PEG Intake

The objective of this study was to determine whether lambs would consume PEG when fed a high-tannin diet and adjust their intake of PEG as the tannin content of the diet changed. We used 5-mo-old lambs (commercial crossbreds) naive to quebracho tannin and PEG. Lambs were weaned at 60 d and reared as described above. Preceding the onset of the trials, they were stratified by weight, randomly allocated to five treatments, and placed in individual pens. Lambs in treatments (n = 6) received a ground test diet with either 0, 5, 10, 15, or 20% quebracho tannin (Tannin Corporation, Peabody, MA). The 0% tannin ration was 30% barley and 70% alfalfa. Tannin replaced alfalfa as the tannin content of the diet increased; hence, the 20% tannin ration was 30% barley, 50% alfalfa, and 20% tannin. Each day from 0900 to 1700, lambs had free access to their treatment ration and they were offered 500 g of PEG in plastic containers. Intake of food and PEG were determined daily for 7 d.

Lambs ate PEG during the self-regulation trial. To determine if lambs would continue to eat PEG when tannin was no longer present, the tannin was removed from all rations. Each day for 3 d from 0900 to 1700, lambs had free access to a ground ration of 30% barley and 70% alfalfa, and they were offered 500 g of PEG. Food and PEG intake were calculated daily. For the next 4 d, lambs had free access to alfalfa pellets 24 h/d, and they were offered 500 g of PEG from 0900 to 1700 daily. Polyethylene glycol consumption was determined daily.

Ten lambs continued to eat PEG after tannin was removed from their ration (five lambs from the 20% tannin group, one lamb from 15% tannin group, and two lambs each from the 10% and 5% tannin groups). The lambs were tested 1 mo after the end of the trial to see if they continued to eat PEG when offered foods without tannin. On d 1, each lamb was offered 2,000 g of alfalfa pellets, 300 g of beet pulp and barley, and 500 g of PEG from 0900 to 1700. Barley and beet pulp were increased to 400 g on d 2, and they were further increased to 450 g on d 3. The amount of PEG and alfalfa offered remained the same for all 3 d. On d 4 to 6, lambs had free access to alfalfa pellets and received 500 g PEG from 0900 to 1700.

Statistical Analyses

The repeated measures analysis of variance for the dosage trial had five treatments (dosages). Lambs (7/treatment) were nested within treatments. Day (n = 10) was the repeated measure. We also used regression analysis to describe the relationship between dose of PEG and mean food intake by lambs in the different treatments. The repeated measures analyses of variance for the self-regulation study had five treatments (tannin levels); we conducted a separate analysis for each of three responses (intake of PEG, ration, and tannin). Lambs (6/treatment) were nested within treatments. Day (n = 7) was the repeated measure. We also compared the intake of PEG by the 10 lambs that ate large amounts of PEG while they were eating the high-tannin diet and 6 wk later; the analysis had two dates and goats were nested within dates. Least significant differences ($\mathbf{LSD}_{.05}$) were determined when *F*-ratios were significant ($P < .05$).

Results

Dose of PEG

There was a linear relationship ($Y = 272 + 1.2X$; $R^2 = 0.86$; $P = .023$) between the amount of supplemental

Table 1. Intake of ground milo grain containing 20% quebracho tannin by lambs supplemented with different amounts of polyethylene glycol (PEG)

Supplemental PEG, g/lamb·d^{-1}	20% Milo-tannin food
0	274[a]
25	320[ab]
50	303[ab]
75	354[bc]
100	407[c]

[a,b,c]Means lacking common superscript letters differ (LSD$_{.10}$).

PEG ingested by lambs and intake of milo-tannin, which generally increased as intake of PEG increased (Table 1; P = .046).

Self-Regulation of PEG Intake

Effect of Tannin on PEG Consumption. As the tannin content of the diet increased (from 0 to 5, 10, 15, or 20%), intake of PEG by lambs also increased (from 9 to 83, 50, 59, and 149 g/lamb·d^{-1}; P = .041; LSD$_{.05}$ = 61). Control lambs ate little PEG throughout the trial, whereas lambs fed the 20% tannin ration ate the most PEG throughout the trial. Generally, lambs fed tannin diets ate more PEG than controls (treatment × day interaction, P = .032; Figure 1).

Individual Variation in PEG Consumption. Intake of PEG varied among lambs fed 5% or 10% tannin. Two lambs fed 5% tannin and one lamb fed 10% tannin ate in excess of 200 g/d of PEG by the end of the trial. However, four lambs in these groups did not eat PEG during the trial. The remaining lambs ate less than 15 g/d of PEG by the end of the trial.

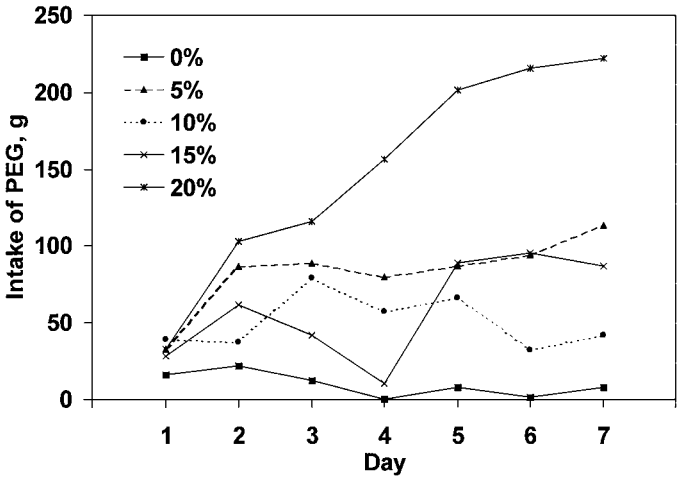

Figure 1. Intake (SEM = 25; LSD$_{.05}$ = 50 g) of polyethylene glycol (PEG) by lambs given ad libitum access to a ground barley-ground alfalfa feed containing 0, 5, 10, 15, or 20% tannin. Lambs had free access to the feed from 0900 to 1700 daily.

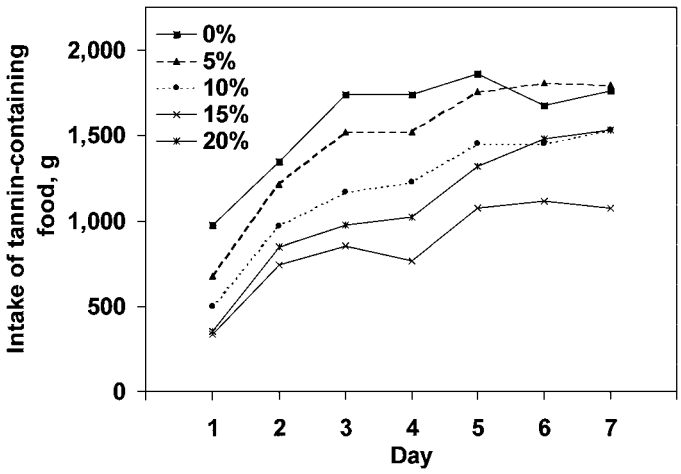

Figure 2. Intake (SEM = 80; LSD$_{.05}$ = 158 g) by lambs of a ground barley-ground alfalfa feed containing 0, 5, 10, 15, or 20% tannin. Lambs had free access to the feed from 0900 to 1700 daily.

Results were less variable in the other groups. Control lambs ate little PEG (<40 g/d) early in the trial and consumed less than 10 g/d by the end of the trial. All lambs fed 15% tannin ate PEG at some time during the trial but their intake was cyclic. All lambs fed 20% tannin increased consumption of PEG throughout the trial. By the end of the trial, two lambs in this group ate in excess of 200 g/d of PEG and the remaining lambs ate in excess of 100 g/d of PEG.

Effect of Tannin on Food Intake. Tannin concentration (from 0 to 5, 10, 15, or 20%) decreased food intake (from 1586 to 1471, 1184, 852, and 1075 g/d; P = .0001; LSD$_{.05}$ = 196 g/d). Food intake increased during the 7-d trial (treatment × day interaction, P = .0651; Figure 2). In general, control lambs ate more than lambs fed diets with 10, 15, or 20% tannin over all 7 d. Lambs fed 15% tannin ate the least during the trial. Lambs fed 5% ate less than did controls on d 1, 3, and 4.

Effect of Tannin on Tannin Intake. Tannin concentration (from 0 to 5, 10, 15, or 20%) increased tannin intake (from 0 to 74, 118, 128, and 215 g; P = .0001; LSD$_{.05}$ = 29 g). Lambs fed 5% tannin ingested less tannin than lambs fed 10 or 15% tannin, and they ingested less tannin than lambs fed 20%. Tannin intake increased throughout the 7-d trial (treatment × day interaction, P = .0001; Figure 3).

Effect of Removing Tannin from the Diet on PEG Intake. For the 7 d immediately after tannin was removed from the diet, lambs previously fed 20% tannin ate more PEG than lambs fed the other rations (P = .0075; Figure 4). Ten of the lambs (5 from 20%, 1 from 15%, and 2 each from 10 and 5% tannin) also continued to eat large amounts of PEG for 7 d after tannin was removed from their diet (Figure 5, d 8 to 14). These

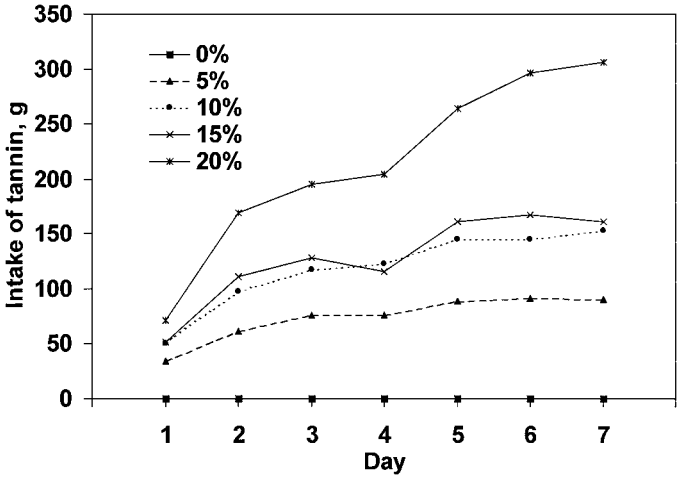

Figure 3. Intake (SEM = 12; $LSD_{.05}$ = 24 g) of tannin by lambs fed diets containing 0, 5, 10, 15, or 20% tannin. Lambs had free access to the feed from 0900 to 1700 daily.

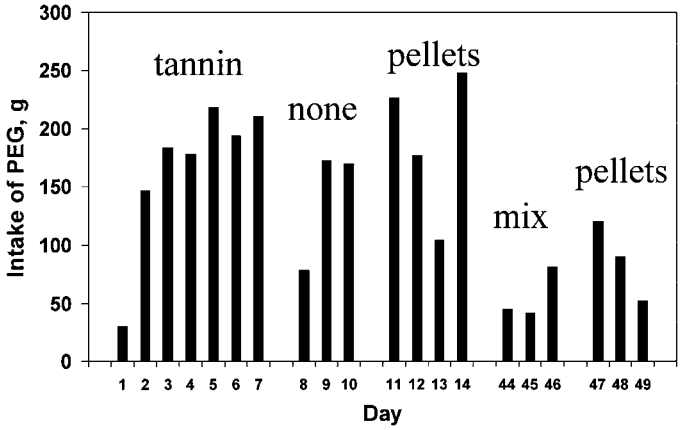

Figure 5. Intake (SEM = 37; $LSD_{.05}$ = 73 g) of polyethylene glycol (PEG) for a subset of 10 lambs that ate the most PEG throughout the trial. From left to right: 1) when the lambs were fed diets with 0, 5, 10, 15, or 20% tannin (d 1 to 7), 2) immediately after lambs were fed the high-tannin diets (d 8 to 10 and 11 to 14), and 3) 6 wk after lambs were fed the high-tannin diets (d 44 to 49). During period "none," lambs were fed the same basal diet as on d 1 to 7. During periods marked "pellets" (d 11 to 14 and 47 to 49), lambs were fed alfalfa pellets. During period "mix," lambs were fed alfalfa pellets, beet pulp, and barley. Lambs had free access to the feeds from 0900 to 1700 daily.

lambs decreased PEG consumption only on d 8 and 13 (Figure 5). However, when offered tannin-free diets 6 wk after the trial (Figure 5, d 44 to 49), intake of PEG had decreased significantly.

Discussion

Dose of PEG

Supplemental PEG increased intake of milo-tannin, but not to the extent of some of our previous studies (Silanikove et al., 1994). Lambs supplemented with 100 g of PEG ate 133 g more of milo-tannin than did controls. Considering that they were eating more than 2.5 kg of food/d, supplemented lambs increased total food intake (milo plus alfalfa) by merely 5%. Thus, PEG supplementation, regardless of dosage, did not increase total food intake markedly when an alternative food (alfalfa pellets) was available later in the day. Polyethylene glycol might have had a greater effect on milo-tannin intake if milo-tannin had been offered for a longer duration each day or if alfalfa pellets had been restricted. Lambs eat more sagebrush when it is offered for several hours each day and when their basal ration of alfalfa pellets is restricted (Banner et al., 2000). Lambs that received PEG may have limited intake of milo-tannin because an alternative food (alfalfa pellets) with an energy content similar to milo-tannin (2.7 vs 2.8 Mcal/kg DE, respectively) was freely available later in the day. In that sense, this experiment is a conservative estimate of the effects of PEG on intake of milo-tannin.

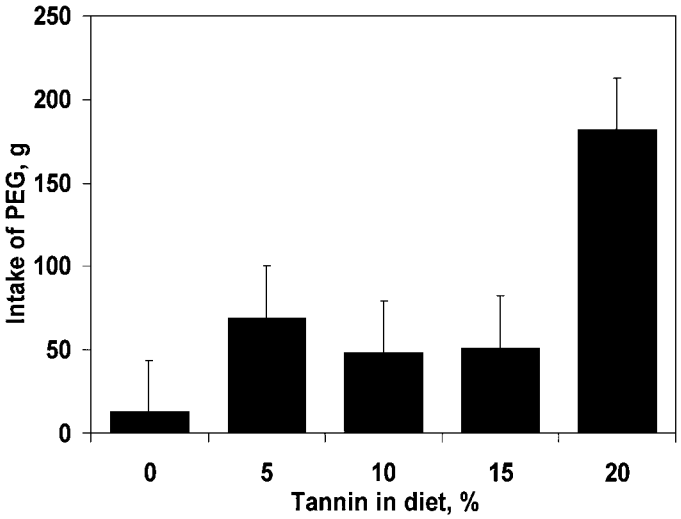

Figure 4. Intake (SEM = 31; $LSD_{.05}$ = 63 g) of polyethylene glycol (PEG) by lambs in all treatments previously fed diets containing 0, 5, 10, 15, or 20% tannin. Lambs had free access to the feed from 0900 to 1700 daily.

Self-Regulation of PEG Intake

All lambs ate similar (low) amounts of PEG on the first day of the trial. Control lambs never did increase intake of PEG during the trial, presumably because they were not experiencing the aversive effects of tannins, and because PEG contains no nutrients. Conversely, intake of PEG increased as the trial pro-

gressed for lambs fed tannin-containing diets. Lambs fed 20% tannin ate the most PEG throughout the trial.

Intake increased as the dosage of PEG increased from 0 to 100 g/lamb·d^{-1} in the dosage study. By comparison, the average animal fed a tannin ration in the self-regulation study ate 85 g/lamb·d^{-1} of PEG, a value well within the range shown to increase intake in the dosage study. As with the dosage study, as we increased the amount of tannin in the ration in the self-regulation study, intake of PEG generally increased.

Lack of preference for the high-tannin food and intake of PEG were likely interrelated. Preference for a food's flavor declines as nutrient content decreases or as toxin content increases (Provenza, 1995). The more inadequate the food in nutrients or excessive in toxins, the stronger the decrease in preference for the flavor (Provenza, 1996; sheep: Wang and Provenza, 1996; Early and Provenza, 1998). As preference declines, animals begin to sample other foods. Thus, a food's chemical characteristics influence the degree to which animals become satiated on its flavor; this, in turn, influences how readily animals sample new foods. In the present study, lambs fed the tannin-containing diets quickly increased intake of PEG compared with controls. We submit that the decrease in nutrients and increase in tannins caused lambs to sample the other "food", PEG. Lambs fed 20% tannin ate food with the lowest nutrient and the highest tannin concentrations, and they ate the most PEG. Polyethylene glycol intake by lambs in other groups was lower and more variable. The level of nutrient deprivation animals must experience before they begin searching for dietary alternatives likely varies from animal to animal and with the diet. Had the trial continued, PEG intake by lambs receiving 10 or 15% tannin may have increased as the lambs became increasingly nutrient deprived.

Some lambs eating 10 or 15% tannin had difficulty establishing that PEG was beneficial. Some ate large amounts of the high-tannin diet and PEG for 1 or 2 d, and then on the ensuing day they decreased intake of PEG but continued to eat the high-tannin diet. Consequently, they had cyclic patterns of intake of both the high-tannin diet and the PEG. Given more time, they may have learned that it was necessary to eat PEG each day to attenuate the aversive effects of the high-tannin diet. Clearly, the response to PEG depended on initial conditions. If lambs did not make the proper association initially (e.g., eat tannin food followed by PEG), or if they did not eat enough PEG to attenuate the effects of tannins, then they may have had difficulty associating PEG with recovery from the aversive effects of tannins.

We complicated matters by introducing both of these novel foods, PEG and the high-tannin diet, at the same time. Lambs fed the tannin diets may have consumed PEG more consistently if the tannin diet had been fed to them for a few days prior to offering PEG so they could have learned the consequences of eating the high-tannin food independent of the confounding effect of PEG. Lambs are likely to learn of the effects of PEG best if they first eat a meal of high-tannin food (and presumably experience malaise) and then immediately afterward eat a meal of PEG (which presumably leads to recovery from malaise). In subsequent work (Villalba and Provenza, unpublished data), we trained lambs to eat PEG by first offering a PEG-grain mixture following consumption of a high-tannin diet; after a few days, we removed the grain. Using this procedure, lambs quickly learned of the beneficial effects of PEG, and they readily accepted PEG from the start because it was mixed initially with a nutritious, familiar food (ground grain). Subsequent removal of the grain did not cause a decrease in intake of PEG. More needs to be learned about how animals learn most efficiently about medicinal effects.

Ten of the lambs (five from 20%, one from 15% and two each from 5 and 10% tannin) continued to eat large amounts of PEG for 7 d after tannin was removed from the ration. These lambs may have been experiencing the effects of tannins that remained in their bodies after the tannin was removed from their diet. The retention time of quebracho tannin in the gastrointestinal tract may be from 48 h (free and soluble) to 72 h (bound to protein and fiber); bound tannin may hydrolyse in the abomasum, and a considerable portion of the neutralizing effect of PEG is exerted in the intestine (Silanikove et al., 1994, 1996). Thus, lambs may have been attenuating the ongoing aversive effects of tannins by continuing to ingest PEG.

Lambs also may have acquired a preference for PEG, which could arise in either of two ways. Lambs may confuse the effects of PEG with the effects of macronutrients, given that PEG likely enhances availability of macronutrients. Alternatively, lambs may learn that PEG attenuates malaise. In addition, when we offered lambs with the highest preference for PEG a tannin-free diet and PEG 6 wk after the trial, their consumption of PEG was much lower than when they were eating the tannin-containing diet. This is consistent with the notion that medicines attenuate malaise, but do not cause shift in preference (hedonic shift). Thus, preference for a medicine extinguishs at a faster rate than a preference conditioned with macronutrients. Conversely, when lambs are conditioned to prefer non-nutritive foods and flavors with energy or protein infusions, preferences persist for at least 2 mo, which suggests that lambs acquire a liking (hedonic shift) for the non-nutritive foods or flavors (Villalba and Provenza, 1997a,c).

Finally, self-regulation of intake of PEG was more qualitative than quantitative. This may have been due in part to differences in how lambs experience malaise from the rates of mixture of PEG and tannins in the gastrointestinal tract. The outcome will depend on how rapidly lambs eat, as well as when and in which sequence they eat PEG and tannins. The main qualitative rule seems to be if tannins are in the food, consume PEG. If the food is really high in tannin, eat more

PEG. Thus, quantification works at the extremes (0 and 20% tannin). In the middle, several factors evidently contributed to diminish the quantitative response.

Effects of Tannin and PEG on Food Intake

Tannin influenced food intake throughout the trial. Lambs offered 5% tannin ate less food than did controls during the first 4 d of the trial. When the ration contained at least 10% tannin, treatment lambs ate less than controls throughout the trial. Lambs fed 15% tannin ate the least food throughout the trial, primarily because they ate the least PEG relative to the content of tannin in their diet. They consumed amounts of tannin similar to lambs fed 10%, but, because the concentration of tannin was higher for 15% group, they ate less food than did the 10% group. Lambs fed 20% tannin ingested more PEG and they ate amounts of food similar to lambs fed 10%. Lambs fed 20% tannin ingested twice as much tannin as lambs fed 10% because they ate more PEG. All of the lambs fed 20% consumed at least 100 g of PEG/d by the end of the trial.

Tannins apparently decrease food intake not only by restricting macronutrient availability but also by promoting aversive effects that are attenuated by PEG. The aversive effects of tannins may be due to astringent effects on oral mucosa of the mouth during food ingestion and postingestive effects due to lesions of the gut mucosa and toxicity (Kumar and Singh, 1984; Reed, 1995). If quebracho tannins had merely restricted macronutrient availability, PEG should have decreased, not increased, food intake because the binding of tannins by supplemental PEG should have increased macronutrient availability. Moreover, if quebracho tannins had merely decreased digestibility by binding to proteins or diluting the nutritional quality of the foods, we would have expected lambs to increase food intake as tannin levels increased regardless of supplemental PEG. When offered foods such as grape pomace, which contains tannins that are bound to macronutrients and hence not aversive, lambs increase food intake as tannin levels increase (Provenza et al., 1996).

Implications

Providing supplemental polyethylene glycol to livestock can be practical under intensive management on pastures. However, supplementing polyethylene glycol can be difficult under more extensive conditions, such as rangelands where livestock forage over vast acreages. In addition, the amount of supplemental polyethylene glycol and the frequency of supplementing depend on the tannin content of the diet, which varies seasonally and with growing conditions in the environment (e.g., moist vs dry, fertile vs infertile, sunny vs cloudy). Our research demonstrated that sheep can self-regulate their intake of polyethylene glycol. Thus, it may be possible to formulate range blocks that allow herbivores to self-regulate their intake of polyethylene glycol in accord with the tannin content of their diet.

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