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Preference for polyethylene glycol by sheep fed a quebracho tannin diet[1,2]

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ABSTRACT: Tannins decrease food intake by reducing digestion and by causing illness, whereas polyethylene glycol (PEG) attenuates the aversive effects of tannins. Our objective was to determine whether sheep recognize the benefits of ingesting substances such as PEG when consuming tannins. If so, then ingestion of PEG should be 1) PEG-specific, 2) a function of previous experience with recovery from tannin-toxicosis, and 3) dependent on the presence/absence of tannins. During conditioning, lambs in Group 1 (n = 10) were offered a meal of high-tannin food, which presumably caused malaise, and then offered PEG (molecular weight, 3,350), which presumably led to recovery from malaise. Subsequently, lambs ingested a control food (wheat straw) that did not have the "medicinal" effects of PEG in the absence of the tannin diet. In contrast, lambs in Group 2 (n = 10) ingested PEG in the absence of the tannin diet, and they ingested the tannin diet only in association with wheat straw. Ingestion of PEG and straw by both groups of lambs increased as a function of the presence of tannins in the diet ($P < 0.05$). However, when offered a choice among the tannin diet, PEG and straw, or when given the tannin diet and then offered a choice between PEG and straw, lambs trained to associate PEG with tannins ate more PEG than lambs that ingested PEG without tannins ($P < 0.05$). The responses were apparently PEG-specific; straw intake did not differ between groups of lambs during testing ($P > 0.05$), and differences in PEG intake disappeared in the absence of tannins ($P > 0.05$). In summary, our results suggest that lambs fed high-tannin diets discriminated the effects of PEG from those provided by a "nonmedicinal" food (straw). Thus, it may be possible to formulate PEG supplements that allow herbivores to self-regulate intake of PEG under extensive management conditions.

Key Words: Decision Making, Intake, Polyethylene Glycol, Sheep, Tannins

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Introduction

Tannins are phenolic compounds that often reduce digestion by forming stable complexes with proteins and carbohydrates (Hagerman et al., 1992), but the great diversity of tannins in nature restricts generalizations about their effects (Foley et al., 1999). Some tannins, such as quebracho, cause lesions in the gut mucosa (Dawson et al., 1999) and they can be degraded in the gut and absorbed (Robbins et al., 1991), exerting their toxic actions systemically (Mehansho et al., 1987; Provenza et al., 1990). Some tannins cause rapid and dramatic reductions in food intake, likely mediated by emetic mechanisms in the nervous system (Provenza et al., 1990, 1994).

Polyethylene glycol (**PEG**) absorbs condensed tannins (Jones and Mangan, 1977), and PEG has been used to neutralize the negative effects of tannins on food intake and digestibility in sheep, goats, and cattle (Silanikove et al., 1994; Hanningan and McNeill, 1998; Landau et al., 2000a). Sheep increase intake of PEG as tannin concentrations in their diet increase (Provenza et al., 2000), perhaps because they recognize the positive "medicinal" effects of PEG and associate PEG with recovery from the aversive effects of tannins. Sheep fed grain prefer substances such as sodium bicarbonate that attenuate acidosis (Phy and Provenza, 1998), and rats acquire preferences for flavors paired with recuperation from apomorphine-induced illness (Green and Garcia, 1971).

Our objective was to further explore the abilities of sheep to self-regulate intake of PEG. We did so by determining 1) whether lambs experienced with PEG and tannins use PEG to a different extent when fed diets with or without tannins and 2) whether the responses of lambs were specific to PEG.

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Materials and Methods

We conducted the study at the Green Canyon Ecology Center, located at Utah State University in Logan. Twenty 4-mo-old lambs (commercial crossbreds; 38 kg, SEM = 1.2) of both sexes were placed in individual pens. Throughout the study, lambs were fed 1 kg of alfalfa pellets following daily trials, and they had free access to mineralized salt blocks and fresh water.

Familiarization with the Tannin Diet

The tannin-containing diet was formulated using quebracho tannin, a source of condensed tannin extracted from the South-American quebracho tree (*Aspidosperma quebracho*). The effects of quebracho tannin on ruminants are well documented by studies in vitro (e.g., Makkar et al., 1995) and in vivo (e.g., Dawson et al., 1999).

Each day from 0800 to 1500, lambs had free access to a ground test diet with 15% quebracho tannin (Tannin Corp., Peabody, MA), 55% alfalfa hay, and 30% barley. Intake was determined daily for 8 d.

Conditioning with PEG

Two groups of lambs were trained to eat PEG under conditions in which PEG supplied a benefit (i.e., ingestion of PEG while consuming tannins; Group 1) or in which PEG did not supply a benefit (i.e., ingestion of PEG without tannins; Control; Group 2).

Conditioning with a Choice. After the last day of familiarization with the tannin diet, lambs were randomly assigned to two groups (10 animals/group), balanced according to previous intake of the tannin diet. At 0800 each morning for the next 5 d, lambs were offered 300 g of PEG (molecular weight, 3,350; Spectrum Chemical, Los Angeles, CA) and they had free access to the tannin diet (Group 1) or a control diet without tannins (Group 2) (Table 1). Quebracho tannin was replaced by grape pomace, such that the control diet was 15% grape pomace, 55% alfalfa hay, and 30% barley. At 1500 refusals were collected and intake of each diet and PEG was measured.

Sequential Conditioning. During the "choice" conditioning period, lambs were reluctant to eat PEG. Thus, during sequential conditioning a PEG-grain mixture was offered. Lambs were familiar with the grain, and they readily ate the mixture. During the first 6 d of conditioning, lambs received a combination of PEG and ground barley with decreasing proportions of barley: 50:50 (d 1 to 2), 60:40 (d 3 to 4), and 80:20 (d 5 to 6). From d 7 to 13, all lambs were offered PEG without grain.

During sequential conditioning, lambs were first fed the diets and then they were offered PEG. Animals are more likely to learn about the benefits of a medicine when they experience illness and then ingest a medicine that leads to recovery (Provenza et al., 2000). From 0800 to 0900 for 13 d, lambs in Groups 1 and 2 were offered the tannin and control diets, respectively. Immediately after ingesting the diets, all animals were offered PEG for 1 h. Immediately after ingesting PEG, lambs in Groups 1 and 2 again were offered the tannin and control diets, respectively, for 3 h (Table 1). Intake of each diet and PEG was calculated daily.

Testing After Conditioning With PEG

The objective of these series of tests was to determine lambs' intake of PEG as a function of the context in which PEG was experienced during conditioning (e.g., with or without ingesting tannins). All preference tests were conducted from 0800 to 1200 and intake of each diet and PEG was determined. During Test 1 (PEG and Conditioning Diet), all lambs had a choice between PEG and the diet received during conditioning. During Test 2 (PEG and Tannin), all lambs had a choice between the tannin diet and PEG. During Test 3 (PEG and Control During Tannin Infusions), all lambs had a choice between the control diet and PEG from 0800 to 1200; at 0900, they received intraruminal infusions of water (300 mL) with quebracho tannin (125 g). The amount of tannin infused was 65% of the average amount of tannin consumed by both groups during the PEG and Tannin test. After the three tests, all animals were given alfalfa pellets for ad libitum consumption for 10 d to allow for excretion of tannins ingested during conditioning and testing. After this period, all lambs had a choice between the control diet and PEG during Test 4 (PEG and Control Without Tannin) (Table 1).

Conditioning with Wheat Straw

The objective in this section was to train the two groups of lambs used in the previous study to eat a food (wheat straw) that did not bind tannins, and thus did not provide the benefits of PEG, while eating a diet with (Group 2) or without (Group 1) tannins.

Conditioning was conducted as described for PEG (sequential conditioning) but wheat straw (ground through a 1-mm screen) replaced PEG, and the test diets were switched so that lambs in Group 1 received the control diet without tannins and lambs in Group 2 received the 15% tannin diet (Table 1). Thus, only lambs in Group 1 had the opportunity to learn about the benefits of PEG when fed tannins; lambs in Group 2 ate PEG with the control diet and they ate straw with the tannin diet.

Testing After Conditioning with Wheat Straw

During testing, lambs' intake of straw was measured as described for PEG (Testing After Conditioning with PEG), but straw replaced PEG (Table 1).

Testing After Conditioning with PEG and Wheat Straw—with Tannins

The response of lambs to PEG and wheat straw was determined after different tannin challenges. Intake of

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Table 1. Methods and procedures in the study

Group	Conditioning: With PEG	Conditioning: With Straw
	Choice	
1	Tannin[a] + PEG	
2	Control[b] + PEG	
	Sequential	
1	Tannin→PEG→Tannin	Control→Straw→Control
2	Control→PEG→Control	Tannin→Straw→Tannin

Testing After Conditioning with PEG

Test	Group	Procedure	Choice between:
1. PEG and Conditioning Diet	1		PEG + Tannin
	2		PEG + Control
2. PEG and Tannin	1, 2		PEG +Tannin
3. PEG and Control During Tannin Infusions	1, 2	After 1 h, intraruminal infusions of tannins	PEG + Control
4. PEG and Control Without Tannin	1, 2	After 10 d of alfalfa pellets *ad libitum*	PEG + Control

Testing After Conditioning With Straw

Same as Testing After Conditioning with PEG but Straw replaced PEG

Testing After Conditioning with PEG and Straw—With Tannins

Test	Group	Procedure	Choice between:
5. Three-way	1, 2		Tannin + PEG + Straw
6. Post-Tannin Meal	1, 2	Before testing, 4-h meal of the tannin food	PEG + Straw
7. Post-Tannin Infusion	1, 2	Before testing, 1-h meal of the control food, followed by infusions of tannins	PEG + Straw

Testing After Conditioning with PEG and Straw—Without Tannins

After 10 d of alfalfa pellets *ad libitum*, same as With Tannins, but Control replaced Tannins (Tests 5 and 6) and water replaced tannin infusions (Test 7).

[a]15% quebracho tannin, 55% alfalfa hay, and 30% barley grain.
[b]15% grape pomace, 55% alfalfa hay, and 30% barley grain.

PEG and straw were assessed during three tests, each one for 4 d. During Test 5 (Three-way), lambs received the tannin diet, PEG, and straw simultaneously from 0800 to 0900. During Test 6 (Post-Tannin Meal), lambs were offered the tannin diet from 0800 to 1200. At 1200, all animals were offered PEG and straw simultaneously for 1 h. During Test 7 (Post-Tannin Infusion), all lambs were offered the control diet from 0800 to 0900. Immediately after collecting the orts, all lambs were given by gavage intraruminal infusions of water (300 mL) containing tannins (60 g). After 30 min, all lambs were offered PEG and straw simultaneously for 1 h. On ensuing days, the amount of tannins infused was 60 (d 2), 90 (d 3), and 100 g (d 4).

Testing After Conditioning with PEG and Wheat Straw—without Tannins

After testing with tannin infusions, all animals were given alfalfa pellets ad libitum consumption for 10 d to allow for excretion of tannins ingested or infused during testing (Silanikove et al., 1994, 1996a). Tests were then conducted, as described in the previous section, but the control diet replaced the tannin diet for Tests 5 and 6. For Test 7, all lambs received intraruminal infusions of 300 mL of water but no tannins.

Statistical Analyses

Intake of foods and supplements during conditioning and testing was analyzed as a split-plot design with animals nested within groups. Group (1 or 2) was the between-subject factor and day was the repeated measure in all of the analyses.

Results

Familiarization to Tannin

Lambs consumed 270 g (SEM = 10) of the tannin diet during the 8-d familiarization period.

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Conditioning with PEG

Conditioning with a Choice. Lambs in Groups 1 and 2 did not differ in their intake of PEG (77 vs 59 g; SEM = 26; $P > 0.05$).

Intake of the tannin diet by lambs in Group 1 was lower than intake of the control diet by lambs in Group 2 (642 vs 1,033 g; SEM = 62; $P < 0.001$).

Sequential Conditioning. Lambs offered the tannin diet (Group 1) ate more PEG than lambs offered the control diet (Group 2) (201 vs 104 g; SEM = 16; $P < 0.001$). Differences in PEG intake between groups became increasingly apparent as conditioning progressed, except for d 11 (group × day interaction; $P < 0.05$; Figure 1).

Averaged across days, intake of the tannin diet by lambs in Group 1 was lower than intake of the control diet by lambs in Group 2 (1,191 vs 1,494 g; SEM = 81; $P < 0.05$). However, intake of the two diets converged during conditioning and diet intake did not differ on d 11 (group × day interaction; $P < 0.001$; Figure 1).

Conditioning with Wheat Straw

Lambs exposed to the tannin (Group 2) and control (Group 1) diets ate similar amounts of wheat straw (96 vs 67 g; SEM = 16; $P > 0.05$). Straw intake did not differ between groups during the first 5 d of conditioning ($P > 0.05$), but as conditioning progressed, lambs in Group 2 ate more straw than lambs in Group 1 (group × day interaction; $P < 0.05$; Figure 1). Averaged across days, intake of the tannin diet by lambs in Group 2 was lower than intake of the control diet by lambs in Group 1 (601 vs 1,686 g; SEM = 68; $P < 0.001$; Figure 1).

Testing After Conditioning with PEG

When PEG was offered in a choice with the diet ingested during conditioning, lambs that received PEG and tannins (Group 1) ate more PEG than lambs that received PEG and the control diet (Group 2) ($P < 0.001$; Figure 2, Test 1). When lambs had a choice between the tannin diet and PEG, they consumed similar amounts of PEG ($P > 0.05$; Figure 2, Test 2). When they were given intraruminal infusions of tannins, and then offered a choice between the control diet and PEG, lambs in Group 1 ate more PEG than lambs in Group 2 ($P < 0.001$; Figure 2, Test 3). When lambs had a choice between the control diet and PEG after 10 d of consuming alfalfa pellets, they consumed similar amounts of PEG ($P > 0.05$; Figure 2, Test 4).

During the choice between PEG and the conditioning diet (Test 1), intake of the control diet by lambs in Group 2 was higher than intake of the tannin diet by lambs in Group 1 ($P < 0.001$, Table 2). In contrast, during the PEG and Tannin test (Test 2), intake of the tannin diet was higher for lambs in Group 1 than for those in Group 2 ($P < 0.001$, Table 2), likely because at this stage lambs in Group 2 had less experience with eating tannins than those in Group 1. During tannin infusions (Test 3), consumption of the control diet did not differ by group ($P > 0.05$), but after 10 d of alfalfa pellets consumed ad libitum (Test 4) it was higher for Group 1 ($P < 0.001$, Table 2).

Testing After Conditioning with Wheat Straw

When straw was offered with the diet ingested during conditioning, lambs offered straw and tannins (Group 2) ate more straw than lambs offered straw and the control diet (Group 1) ($P < 0.001$; Figure 2, Test 1). When both groups had a choice between the tannin diet and straw (Test 2), or between the control diet and straw while receiving infusions of tannins (Test 3), Group 2 ate more straw than Group 1 ($P < 0.001$; Figure 2). When Groups 1 and 2 had a choice between the control diet and straw after 10 d of consuming alfalfa pellets, they ate similar amounts of straw ($P > 0.05$; Figure 2, Test 4).

During the choice between straw and the conditioning diet (Test 1), intake of the control diet by lambs in Group 1 was higher than intake of the tannin diet by lambs in Group 2 ($P < 0.001$, Table 2). During Tests 2 (Straw and Tannin) and 3 (Tannin Infusions), intake of the tannin and control diets, respectively, was higher for Group 1 than for Group 2 ($P < 0.001$). After 10 d of consuming alfalfa pellets ad libitum (Test 4), intake of the control diet did not differ between groups ($P > 0.05$; Table 2).

Testing After Conditioning with PEG and Wheat Straw—with Tannins

When given a choice between the tannin diet, PEG, and straw, lambs previously conditioned with tannins and PEG (Group 1) consumed more PEG than lambs previously conditioned with the control diet and PEG (Group 2) ($P < 0.05$; Figure 3, Test 5). Likewise, when all lambs had the tannin diet for 4 h and then had a choice of PEG and straw, lambs in Group 1 ate more PEG than did lambs in Group 2 ($P < 0.05$; Figure 3, Test 6). When lambs were infused with increasing doses of tannins, there were no differences in PEG intake between groups ($P > 0.05$; Figure 3, Test 7).

There were no differences in straw intake between groups of lambs for any of the three testing periods ($P > 0.05$; Figure 3), nor did diet consumption differ between groups ($P > 0.05$; Table 2).

Testing After Conditioning with PEG and Wheat Straw—without Tannins

When tannins were absent from the diets (Three-way and Post-Control Meal) and from the infusions (Post-Water Infusion), no differences in PEG or straw intake were detected between groups of lambs ($P > 0.05$; Figure 3), nor were there differences in intake of the control diet by the two groups of lambs ($P > 0.05$; Table 2).

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Discussion

Ability of Lambs to Learn about the Effects of PEG

We hypothesized that if sheep recognize the benefits of ingesting PEG paired with recovery from illness due to tannins, then ingestion of PEG should be 1) PEG-specific, 2) a function of previous experience with recovery from tannin-toxicosis, and 3) dependent on the presence/absence of tannins. Results of post-conditioning tests were consistent with these predictions. When offered the tannin diet, PEG, and straw in a choice, or when fed the tannin diet and then offered a choice between PEG and straw, lambs trained to associate PEG with tannins ate more PEG than lambs that ingested PEG without tannins during conditioning. These responses were apparently PEG-specific, because they did not occur when straw replaced PEG (Figure 3). Finally, differences in PEG intake occurred only when lambs consumed the tannin diet during (Three-way) or before (Post-Tannin Meal) testing. When tannins were absent from the diet, intake of

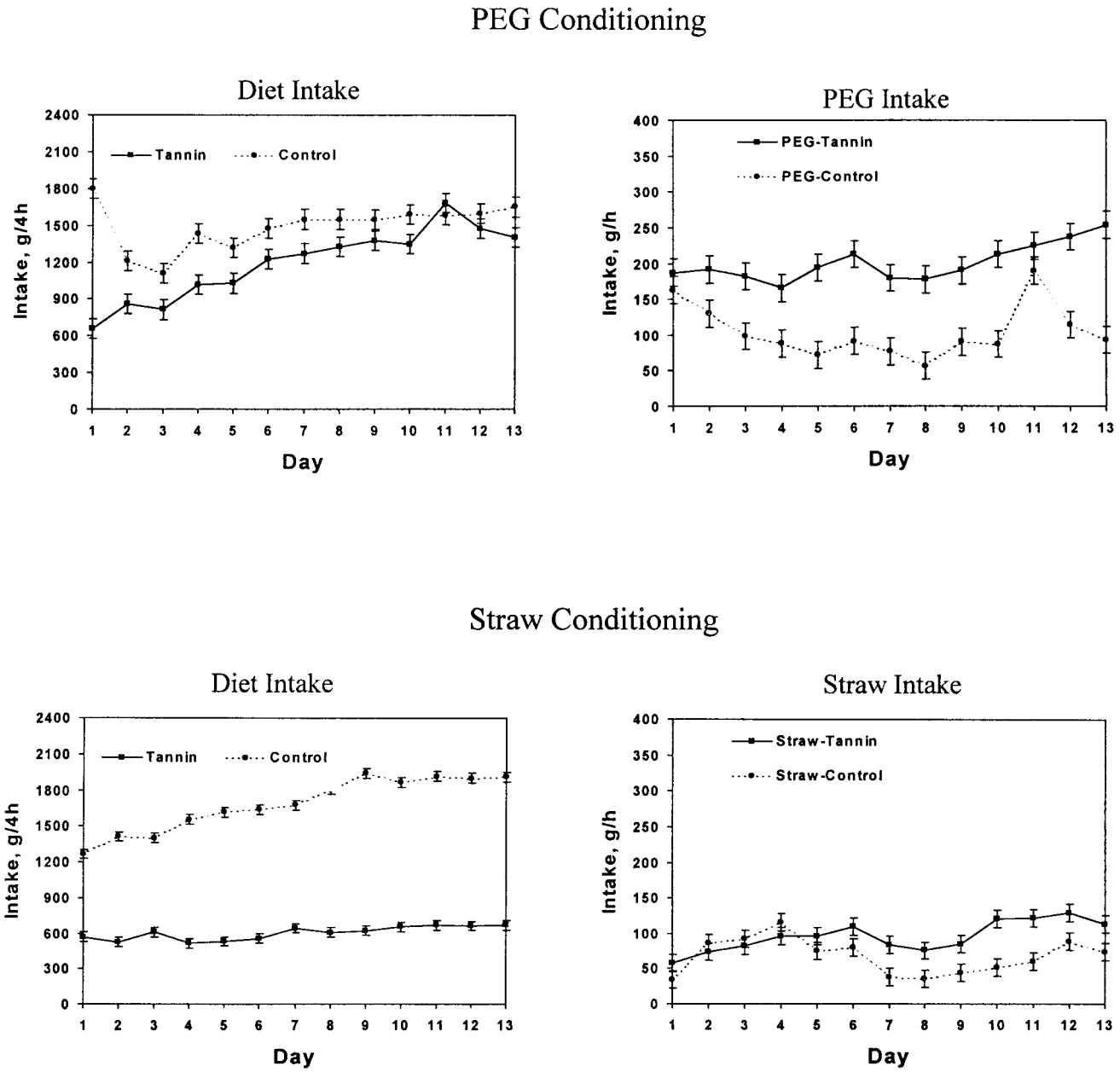

Figure 1. Intake of a diet with (Tannin) or without (Control) 15% quebracho tannin, polyethylene glycol (PEG), and straw by two groups of lambs during two conditioning periods. During conditioning with PEG, lambs had the tannin diet (Group 1) or the control diet (Group 2) before (1 h) and after (3 h) receiving PEG for 1 h. During conditioning with straw, the diets were switched and wheat straw replaced PEG. Values are means for 10 animals; standard errors are represented by vertical bars.

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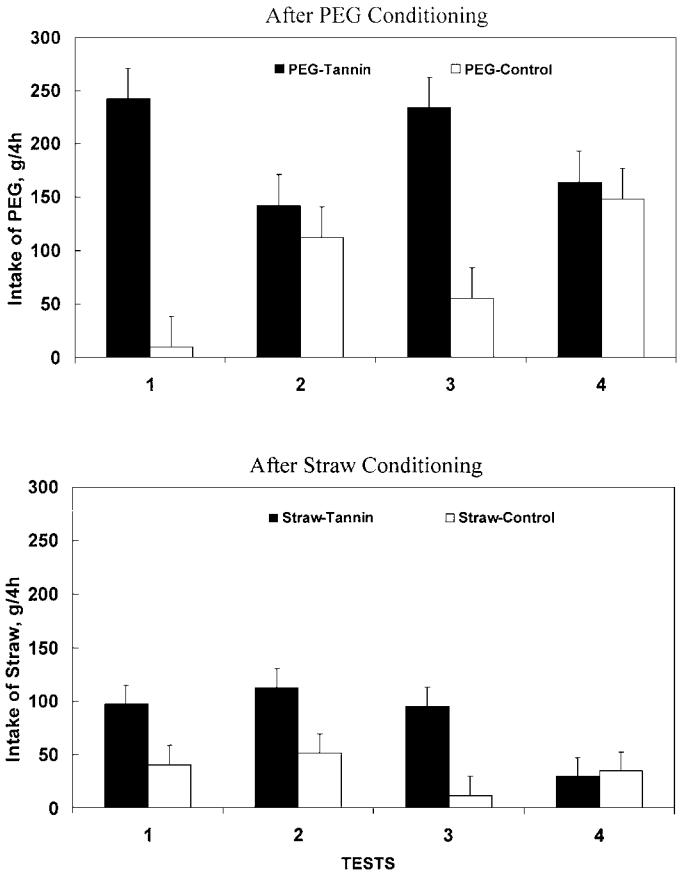

Figure 2. Intake of polyethylene glycol (PEG) and straw by two groups of lambs after two conditioning periods in which lambs were trained to associate PEG or wheat straw with a 15% quebracho tannin diet (PEG-Tannin; Straw-Tannin) or control diet without tannin (PEG-control; Straw-Control). Lambs had a choice between PEG (after PEG conditioning) or straw (after straw conditioning) and 1) their conditioning diets (Test 1), 2) the tannin diet (Test 2), 3) the control diet while receiving intraruminal infusions of tannins (Test 3), or 4) the control diet after 10 d of consuming alfalfa pellets (Test 4). Values are means for 10 animals; standard errors are represented by vertical bars.

PEG was not affected by the lambs' previous conditioning history (Figure 3).

All lambs were naïve to PEG initially, and thus they ate small amounts of PEG. Acceptance of PEG increased when PEG was mixed with ground barley, a nutritious, familiar food. Removal of barley did not cause a decrease in intake of PEG, even though PEG has no nutritional value (Bauman et al., 1971). However, PEG is not completely neutral in the GI tract, because it increases osmolality of the digesta.

Lambs also continued to eat straw after removal of the barley. However, intake declined, especially for lambs fed the control diet (Figure 1).

Mere exposure can enhance acceptance of food (Zajonc, 1968), and some studies suggest that novel foods become more palatable with increasing exposure (Pliner, 1982). The more extensive exposure to PEG and straw, along with the lack of preference for the tannin diet, helps explain why lambs that consumed tannins ate more PEG and straw during conditioning (Figures 1 and 2). When lambs were offered choices between the control diet and PEG or straw after 10 d of receiving alfalfa pellets, these differences disappeared (Figure 2). The retention time of quebracho tannin in the gastrointestinal tract ranges from 48 h (free and soluble) to 72 h (bound to protein and fiber) (Silanikove et al., 1994, 1996a). Thus, after 10 d of eating alfalfa pellets, all lambs presumably had excreted all of the ingested tannins.

In a previous study, lambs ate PEG in amounts proportional to the tannin content of their diets (Provenza et al., 2000). The design of that study did not enable us to determine whether the response was due to decreased preference for tannins in the diet and sampling for potentially better alternative foods or was a specific response to the effects of PEG on tannins. The inclusion of a control food (straw) and a conditioning protocol with different associations between test foods and tannins allowed us to discriminate between the ingestion of a familiar, safe food (straw) and a substance that supplies a benefit (PEG). The inclusion of familiar, safe foods has been used to identify preferences for flavors paired with recovery from illness in rats (Zahorik et al., 1974).

It is likely that the different sensorial properties of PEG and straw helped lambs discriminate between these two foods. Polyethylene glycol is crystalline and straw is fibrous and, at least to humans, they differ in their taste. After sensory discrimination occurred, the postingestive consequences of ingesting both foods with tannins calibrated intake values according to the foods' utilities (Figures 2 and 3).

Collectively, our results suggest that sheep discriminated substances that supplied a benefit (PEG) from those that did not (straw). Sheep fed acid-producing substrates such as grain subsequently prefer foods and solutions containing substances such as sodium bicarbonate and lasalocid that attenuate acidosis (Phy and Provenza, 1998).

Ability of Lambs to Recognize the Effects of Tannins

When oral experience with tannins was circumvented by intraruminal infusions, differences in PEG intake between groups of lambs disappeared (Figure 3, Post-Tannin Infusion test). Although it is conceivable that the doses of tannins we used were too low to cause negative postingestive effects, this is unlikely given that even lower doses of quebracho tannin reduce nutrient utilization and affect performance of sheep (Dawson et al., 1999). We used lower doses of tannins after conditioning with PEG and straw than after conditioning with either PEG or straw to reduce the potential negative effects of tannins administered in one pulse for 4 d (Post-Tannin Infusion test) as opposed to 1 d (choices

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between PEG and Control or between straw and Control during tannin infusions).

It is more likely that the postingestive effects of tannins alone are not the only cue ruminants use to identify tannins. Astringency due to the interaction of tannins with salivary and mucosa proteins in the mouth signals the ingestion of tannin-rich diets (Prinz and Lucas, 2000). Precipitation of proteins by tannins increases the friction coefficient of the oral mucosa vs the teeth, which provides a sensitive and rapid detection mechanism for tannin ingestion (Prinz and Lucas, 2000). Polyethylene glycol exchanges with protein in protein-tannin complexes (Jones and Mangan, 1977). Thus, if PEG reduced astringency by releasing protein into the saliva, lambs could have used this cue to selectively increase intake of PEG. Astringency reduces intake of quebracho tannin diets in heifers, and the effect is annulled within minutes by ingesting PEG (Landau et al., 2000b). When tannins were delivered by intraruminal infusion, the oral cue from astringency was absent, and that may have reduced lambs' responses to PEG. Oral experience influences preference (Swithers and Hall, 1994), and the combination of oral and postingestive effects is more important than either alone in food choices (Pérez et al., 1996). The lack of differences in PEG intake between groups of lambs when tannins were absent from the diets also supports the notion that oral experience with tannins was needed for lambs to increase PEG intake (Figure 3, Without Tannins).

During post-tannin infusion tests, lambs in both groups likely ingested PEG due to the postingestive effects of infused tannins. Polyethylene glycol-condensed tannin ratios of 1:2 totally neutralize the negative effects of condensed tannins (Silanikove et al., 1994). During post-tannin infusion tests, all lambs consumed more than enough PEG (200 to 300 g) to neutralize infused tannins (60 to 100 g). Moreover, the high levels of PEG consumed by lambs trained to associate PEG with tannins during post-tannin meal tests might have diminished, due to a carryover effect, the differences in PEG intake between groups in post-tannin infusion tests (Figure 3). Finally, lambs that received the straw-tannin association during conditioning (Group 2) apparently started to learn about the beneficial effects of PEG during the three-way and post-tannin meal tests, as evidenced by their increased intakes

Table 2. Intake (g) of tannin[a] and control[b] diets by two groups of lambs trained to associate PEG (Group 1) or wheat straw (Group 2) with the tannin diet and wheat straw (Group 1) or PEG (Group 2) with the control diet

After Conditioning with PEG	Test[c] 1	2	3	4
Group 1	Tannin: 948[e]	Tannin: 1,398[e]	Control: 1,174	Control: 955[e]
Group 2	Control: 1,133[f]	1,135[f]	1,130	640[f]
SEM			72	
After Conditioning with Straw				
Group 1	Control: 1,338[e]	Tannin: 1,122[e]	Control: 1,046[e]	Control: 1,082
Group 2	Tannin: 692[f]	682[f]	714[f]	1,017
SEM			92	

After Conditioning with PEG and Straw with Tannins	Test[d] 5	6	7
Group 1	Tannin: 223	Tannin: 830	Control: 655
Group 2	314	797	437
SEM	71	127	89

After Conditioning with PEG and Straw without Tannins	Test[d] 5	6	7
Group 1	Control: 639	Control: 1,485	Control: 613
Group 2	607	1,270	597
SEM	64	141	89

[a]15% quebracho tannin, 55% alfalfa hay, and 30% barley grain.
[b]15% grape pomace, 55% alfalfa hay, and 30% barley grain.
[c]Lambs had a choice between PEG (After Conditioning with PEG) or straw (After Conditioning with Straw) and their conditioning diets (Test 1); the tannin diet (Test 2); the control diet while receiving intraruminal infusions of tannins (Test 3); or the control diet after 10 d of consuming alfalfa pellets (Test 4).
[d]During Test 5, lambs were offered the tannin diet, PEG, and wheat straw. During Test 6, lambs were offered PEG and wheat straw after receiving the tannin diet. During Test 7, lambs were offered PEG and wheat straw after receiving the control diet and intraruminal infusions of tannins (Test 7) (with Tannins). The control diet replaced the tannin diet (Tests 5 and 6) and the vehicle (water) replaced the tannin infusions (Test 7) (without Tannins).
[e,f]Means within a column lacking a common superscript differ ($P < 0.05$).

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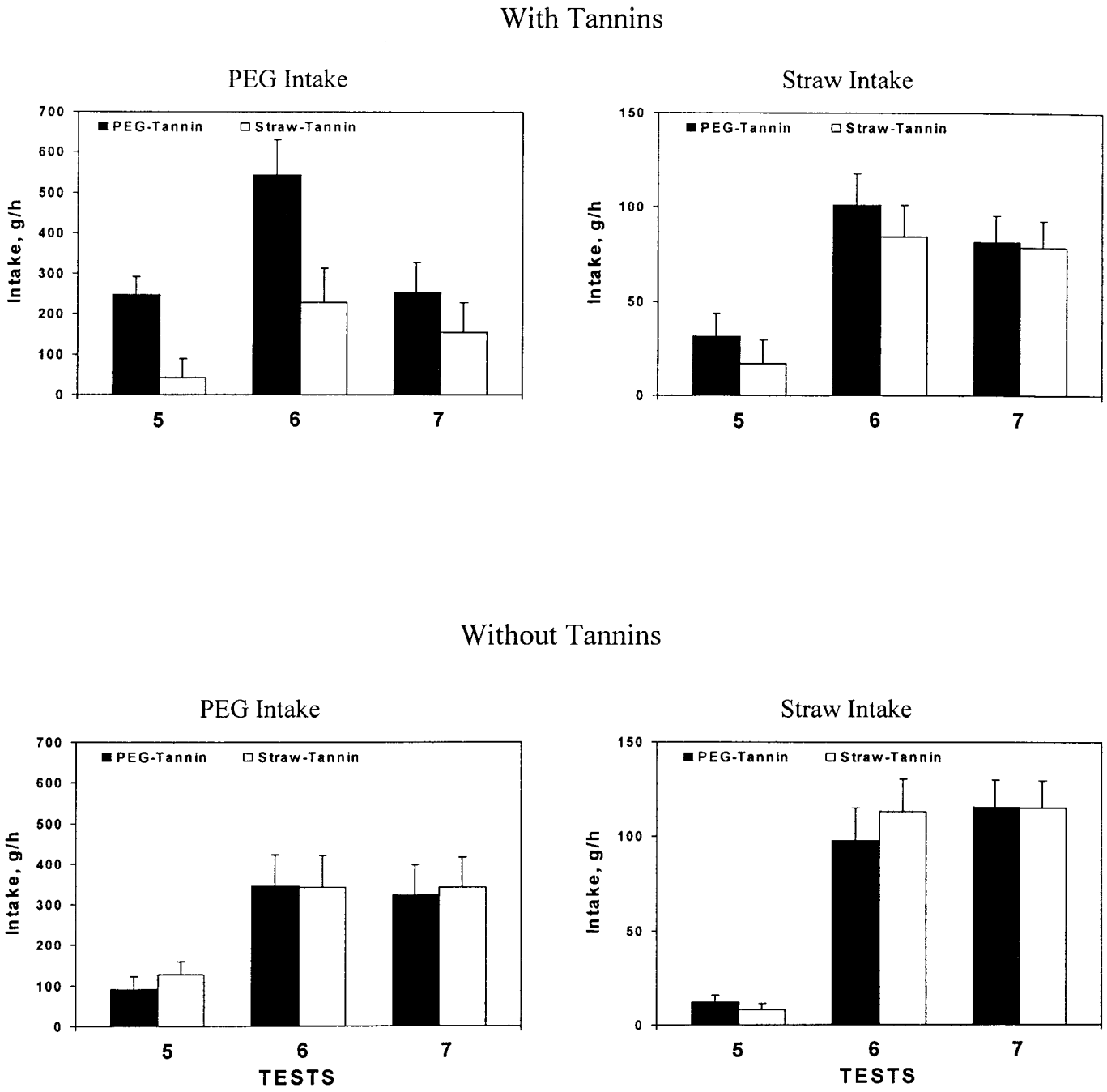

Figure 3. Intake of polyethylene glycol (PEG) and wheat straw by two groups of lambs trained to associate PEG (PEG-Tannin) or wheat straw (Straw-Tannin) with a diet containing 15% quebracho tannin. When testing with tannins, lambs had a simultaneous offer of the tannin diet, PEG, and wheat straw (Test 5); received the tannin diet for 4 h before a simultaneous offer of PEG and wheat straw (Test 6); or received intraruminal infusions of tannins before having a choice between PEG and wheat straw (Test 7). When testing without tannins, lambs were offered alfalfa pellets for 10 d prior to testing. The control diet without tannins replaced the tannin diet (Tests 5 and 6) and intraruminal infusions of water (Test 7) replaced the tannin infusions. Values are means for 10 animals; standard errors are represented by vertical bars.

of PEG across testing (Figure 3). Their ongoing conditioning likely attenuated the differences in PEG intake between groups of lambs as testing proceeded.

Intake of Diets During and After Conditioning

Supplemental PEG increased intake of the tannin diet to levels comparable to those observed with the control diet, especially during the last days of conditioning, and to much higher levels than those attained with straw supplementation (Figure 1). These results are consistent with previous findings (Landau et al., 2000a) and indicate that PEG supplies more benefits than straw for animals fed high-tannin diets. Quebracho tannins decrease food intake by reducing macronutrient

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availability and by eroding the mucosal lining of the gastrointestinal tract (Dawson et al., 1999). The interaction between PEG and tannins apparently occurs by hydrogen bonding between oxygen through an ether linkage of the PEG chain and the phenolic hydroxyl group of the tannin (Silanikove et al., 1996b). This interaction is irreversible over a wide range of pH and renders tannins unavailable for the formation of protein-tannin complexes (Jones and Mangan, 1977) that adversely affect animal tissues and nutrient absorption (Foley et al., 1999).

Implications

Our findings suggest that lambs fed high-tannin diets discriminate the positive effects of polyethylene glycol (PEG) from those provided by a control, "nonmedicinal" food. Increased use of PEG in response to a tannin diet required previous experience with the beneficial effects of PEG. Even though PEG can increase intake of tannin-containing plants, thereby enhancing animal performance, providing supplemental PEG can be labor-intensive under extensive conditions, such as rangelands where livestock are distributed over large areas. Our results suggest that it may be possible to formulate range blocks that allow herbivores to self-regulate intake of PEG.

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