Polyethylene glycol influences selection of foraging location by sheep consuming quebracho tannin

J. J. Villalba and F. D. Provenza

J Anim Sci 2002. 80:1846-1851.

Polyethylene glycol influences selection of foraging location by sheep consuming quebracho tannin[1]

J. J. Villalba[2] and F. D. Provenza

Department of Rangeland Resources, Utah State University, Logan 84322-5230

ABSTRACT: Tannins are a heterogeneous group of phenolic polymers that can induce detrimental effects when consumed by herbivores. Polyethylene glycol (PEG) binds to tannins and thus attenuates their negative effects. Our objective was to determine whether sheep actively seek PEG when fed tannins and thus modify their foraging location as a function of the spatial distribution of PEG. Lambs were first trained to recognize the beneficial effects of PEG by offering a meal high in quebracho tannin (QT), which presumably caused malaise, and then PEG (MW, 3,350), which presumably led to recovery from malaise. Animals were then tested in an experimental area where they could forage at two different locations that contained in Trial 1 1) PEG and QT in adjacent food boxes (PEG+QT) or 2) QT and in Trial 2 1) PEG or 2) QT. Preference for foraging locations was tested under three conditions: 1) no preload meal, 2) a meal high in quebracho tannin 1 h before testing, and 3) a basal diet high in quebracho tannin. Lambs spent more time (P = 0.012) and ate more tannin-containing food (P = 0.022) at locations where PEG was present (PEG+QT) than where it was absent (QT; Trial 1). Lambs responded to increased tannins in their bodies (Conditions 2 and 3) by reducing intake (P = 0.0001; Trial 2) at sites containing only QT and by increasing intake (P = 0.0001, Trial 1; P = 0.001, Trial 2) and foraging time (P = 0.072, Trial 1; P = 0.0001, Trial 2) at locations where PEG was available. Thus, PEG influenced foraging location by sheep consuming quebracho tannin. Accordingly, it may be possible to formulate range blocks that enable herbivores to ingest PEG in tannin-rich habitats. Strategic distribution of PEG in those habitats may attract animals to underutilized feeding sites.

Key Words: Foraging, Intake, Learning, Polyethylene Glycol, Sheep, Tannins

 J. Anim. Sci. 2002. 80:1846–1851

Introduction

Tannins are a heterogeneous group of phenolic polymers common in plants (Hagerman et al., 1992). Tannins can induce detrimental effects when consumed by herbivores. For instance, quebracho, a condensed tannin, reduces digestibilities of DM, N, and NDF and causes epithelial degeneration and ulceration of the gastrointestinal tract when fed to sheep (Dawson et al., 1999).

Polyethylene glycol (**PEG**) is a polymer that can bind tannins irreversibly, and its presence reduces the formation of protein-tannin complexes (Jones and Mangan, 1977). Thus, supplementation with PEG has been used to alleviate the negative effects of tannins on livestock (Landau et al., 2000).

Recent studies suggest that sheep recognize the "medicinal" effects of PEG while ingesting tannin-rich foods. Lambs increase intake of PEG as quebracho tannin concentrations in their diet increase (Provenza et al., 2000), and they discriminate the positive effects of PEG from those provided by control "nonmedicinal" foods (e.g., wheat straw) by selectively increasing intake of PEG after a tannin challenge (Villalba and Provenza, 2001). In these studies sheep were fed quebracho tannins and PEG in confinement, and thus it is not known whether sheep actively seek PEG when fed tannins and thus modify their foraging location as a function of the spatial distribution of PEG. Our objective was to determine 1) whether lambs experienced with the beneficial effects of PEG preferentially used sites with PEG while consuming tannins and 2) whether responses to the spatial distribution of PEG were influenced by the amount of tannin in the diet.

Materials and Methods

We conducted the study at the Green Canyon Ecology Center, located at Utah State University in Logan.

[1]This research was supported by grants from the Utah Agric. Exp. Stn. This paper is published with the approval of the Director, Utah Agric. Exp. Stn., Utah State Univ., Logan, UT, as journal paper number 7423.

[2]Correspondence: (phone: 435-797-2539; fax: 435-797-3796; E-Mail: villalba@cc.usu.edu).

Received November 7, 2001.
Accepted February 6, 2002.

Twenty 4-mo-old lambs (commercial crossbreds; 34 ± 1 kg BW) of both sexes were penned as a group. Lambs had free access to mineralized salt blocks and fresh water throughout the study.

The objective of the study was to determine whether lambs exposed to tannins modify their foraging location as a function of the presence of a substance (PEG) that attenuates the aversive effects of tannins. As the trials progressed, the experience of the lambs with tannins and PEG increased. Herbivores constantly adapt to the environment (Provenza et al., 1998). We show the emergence of some of these adaptive interactions in response to the evolving experimental conditions of the study.

Familiarization with the Experimental Area

Lambs were placed as a group in a 24- × 30-m fenced experimental area for 22 d to allow familiarization with the area and with the future location of the experimental foods. The longer sides of the rectangular area were positioned in an east-west direction and food containers were placed in two locations at the far southernmost corners of the area, one along the west side and the other along the east side. At 0900 daily, lambs were fed an average of 1 kg of alfalfa pellets and 400 g of barley grain/lamb in the experimental area. Every day the feeding location was switched, so that lambs had the same experience with feeding at both locations. At 1300 lambs were penned as a group in an adjacent pen (4 × 30 m) along the north side of the experimental area until the next morning. Following a 22-d familiarization period with the experimental area, lambs were penned individually and each lamb was fed 1 kg of alfalfa pellets following the ingestion of the test foods.

Familiarization with the Tannin-Containing Food

Each day from 0800 to 1200, lambs had free access to a ground test food (1- to 5-mm particle size) with 15% quebracho tannin (Tannin Corp., Peabody, MA), 55% alfalfa hay, and 30% barley. Intake of the food was determined daily for 8 d. During this period, lambs consumed 212 g/d (SEM = 13) of the tannin-containing food.

Conditioning with PEG

We trained lambs to eat PEG under conditions in which they could learn about the benefits of PEG while consuming tannins. To do so, we followed a sequential conditioning protocol (Villalba and Provenza, 2001) in which we first fed the tannin-containing food (1,100 g) and then offered PEG (300 g). From 0900 to 1000 for 18 d, lambs were offered the tannin-containing food. Immediately after ingesting this food, all animals were offered PEG (molecular weight, 3,350; Van Waters & Rogers, Richmond, BC, Canada) for 1 h. Immediately after ingesting PEG, lambs again were offered the tannin-containing food for 3 h. Intake of the tannin food and PEG were calculated daily.

Lambs are reluctant to eat PEG when it is novel (Villalba and Provenza, 2001). Thus, we trained lambs to eat PEG by first offering a PEG-barley grain mixture. Lambs were familiar with the grain, and they readily ate the mixture. During the first 7 d of conditioning, lambs received a combination of PEG and ground barley with decreasing proportions of barley: 50:50 (d 1 to 3), 60:40 (d 4 to 5), and 80:20 (d 6 to 7). From d 8 to 18 all lambs were offered PEG without grain. After conditioning with PEG, lambs (43 ± 1 kg BW) were returned to the experimental area and penned as a group.

Trial 1: Preference for Locations with Tannins vs Locations with Tannins + PEG

The objective of this trial was to determine whether lambs preferred a location that contained tannins and PEG to a location that contains only tannins. We tested preferences for locations containing tannins + PEG or tannins across a gradient of increased tannin concentrations in the diet (No preload, Preload, Basal Diet).

Prior to the trials, we familiarized lambs with the specific locations of PEG and tannins in the experimental area. Pairs of lambs were offered a specific food combination at one location for 7.5 min and then moved to the opposite location and offered the alternative food/s for another 7.5 min. This procedure was repeated three times for each pair of lambs on six consecutive days (a different group each day in an alternate sequence).

No Preload. In order to control for an unspecific preference for a location, pairs of lambs were randomly divided into two groups (10 lambs/group). Because lambs are reluctant to eat in isolation, we formed pairs of lambs at random within each group (five pairs/group) and the pair was considered the experimental unit. Once formed, the same pairs of lambs, identified by specific numbers, always were tested together.

Lambs in Group 1 were offered two containers with the tannin-containing food (500 g/container) and two containers with PEG (300 g/container) on the west side of the experimental area. Containers with PEG and tannins were adjacent and placed in an alternate order. On the east side of the experimental area, lambs in Group 1 had two adjacent containers both with the tannin-containing food (500 g/container). Lambs in Group 2 were offered the same amounts of foods but in opposite locations. The side on which tannins or tannins+PEG occurred remained constant for each pair of lambs throughout the trial.

During daily trials, foods were placed on opposites sides (i.e., east and west) of the experimental area and each pair of lambs was released from the center of the north side of the area (adjacent to the holding pen) and allowed to forage for 15 min. One observer recorded the behavior of each pair of lambs from a distance of approximately 30 m while they foraged. We measured the time lambs spent at each location and excluded bouts of inactivity from calculations of feeding time.

Lambs always stayed at the same location and their actions (i.e., eating or not eating) were syncronized more than 95% of the time. Bouts of inactivity were only considered when both individuals in the pair did not consume food. Each pair of lambs was tested twice on two consecutive days. Lambs from Groups 1 and 2 were tested in a consecutive sequence and the order of testing was reversed on d 2. Testing occurred from 1000 to 1400. After daily tests, we measured intake of PEG and intake of the tannin-containing food. Lambs were penned as a group in the adjacent holding pen until the next day. They received an average of 1 kg of alfalfa pellets per lamb per day as their basal diet.

Preload. Lambs were tested as described in the previous trial, but 1 h before testing all lambs were offered a meal of the tannin food (an average of 1 kg/lamb).

Basal Diet. Lambs were tested as described before, but 2 d before and during testing all lambs were fed a basal diet of the tannin food (ad libitum access), which replaced the basal diet of alfalfa pellets.

Trial 2: Preference for Locations with Tannins vs Locations with PEG

The objective of this trial was to determine lambs' preferences for a location that contained tannins relative to a location that contained PEG. Again, we tested preferences for locations containing tannins or PEG across a gradient of tannin concentrations in the diet (No preload, Preload, Basal Diet).

No Preload. After Trial 1, lambs were offered alfalfa pellets for ad libitum consumption for 5 d. After this period, we familiarized the same pairs of lambs with the locations of PEG and tannins in the experimental area. Pairs of lambs were offered one food at one location for 7.5 min and then moved to the opposite location and offered the alternative food for another 7.5 min. This procedure was repeated two times for each pair of lambs on four consecutive days (a different group of lambs each day in an alternate order).

The location of PEG for each group of lambs was modified in relation to Trial 1. Lambs in Group 1 were offered two adjacent containers with the tannin food (500 g/container) on the west side of the experimental area and two adjacent containers with PEG (300 g/container) on the east side of the area. Lambs in Group 2 were offered the same amounts of foods, but in opposite locations. The side on which tannins and PEG occurred remained constant for each pair throughout the trial.

During daily trials, the tannin food and PEG were placed at opposites sides (e.g., east and west) of the experimental area and each pair of lambs was allowed to forage for 15 min. We used the same protocol and the same number of repetitions described in the previous trial for measuring foraging time and food intake.

Preload. Lambs were tested as described in the previous trial, but 1 h before the choice all lambs were offered a meal of the tannin food (an average of 1 kg/lamb).

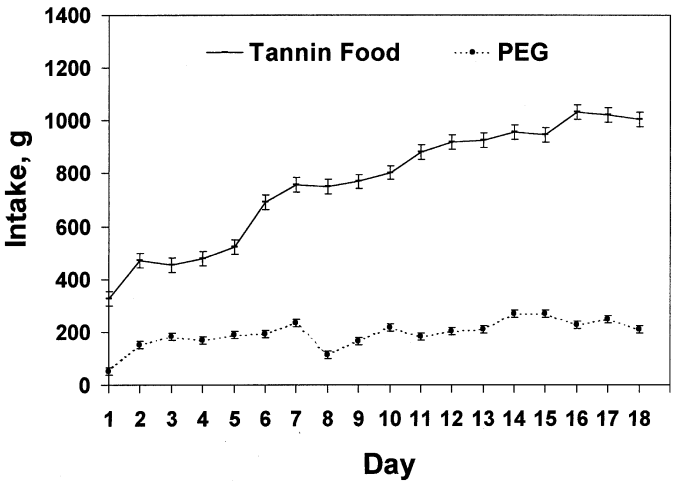

Figure 1. Intake (± SEM) of a food with 15% quebracho tannin (Tannin food) and polyethylene glycol (PEG) by lambs during conditioning. Lambs received the tannin food for 1 h, followed by PEG for 1 h and then the tannin food for 3 h. From d 1 to 7 PEG was mixed with barley grain and from d 8 to 18 PEG was offered without grain.

Basal Diet. Lambs were tested as described before, but 2 d before and during testing all lambs were fed a basal diet of the tannin food (ad libitum access), which replaced the basal diet of alfalfa pellets.

Statistical Analyses

Intake of the tannin food and PEG during conditioning (with PEG) was analyzed as a repeated measures design with lambs (20) as the between-subject factor and day (18) as the within-subject factor.

Intake of the tannin food, PEG, and feeding time were analyzed as a split-plot design with pairs of lambs nested within groups. Group (1 or 2) was the between-subject factor, and location was the within-lamb factor. Day (1–2) and Period (No Preload, Preload, Basal Diet) were the repeated measures in the analysis. Means were compared using the LSD test. The ANOVA was performed using the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC).

Results

Conditioning with PEG

Intake of the tannin-containing food and PEG during conditioning is shown in Figure 1. Intake of the tannin-containing food differed across days (day effect; $P = 0.0001$). When grain was no longer fed in a mixture with PEG (d 8), lambs decreased their intake of PEG relative to previous days (day effect; $P < 0.0001$), but after d 10 animals consumed PEG at levels comparable to those when PEG was mixed with grain (Figure 1).

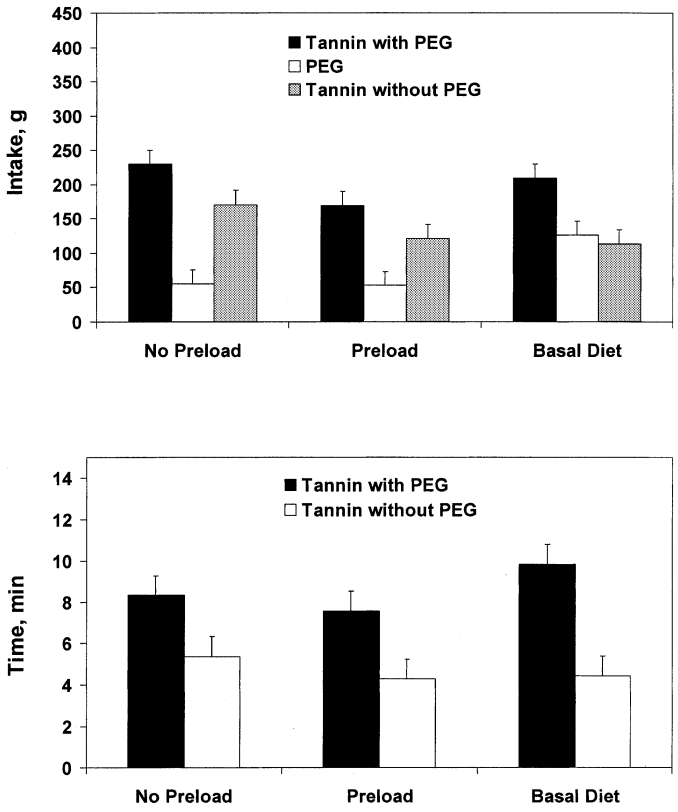

Figure 2. Intake (± SEM) of a food with 15% quebracho tannin and polyethylene glycol (PEG) at two different locations, and time (± SEM) spent at those locations by two groups of lambs. Lambs could choose between a location that contained the tannin food and PEG in adjacent food containers (Tannin with PEG) and another location that contained only the tannin food (Tannin without PEG). Tests were conducted across a gradient of increased tannin concentrations in the lambs' diet (No preload; Preload: 1-h meal of the tannin food before testing; Basal Diet: The tannin food replaced a basal diet of alfalfa pellets).

Trial 1: Preference for Locations with Tannins vs Locations with Tannins + PEG

Intake of the Tannin-Containing Food. The presence of PEG influenced lambs' ingestion of the tannin-containing food (Figure 2). Averaged across periods, lambs' intake of the tannin food was higher at the location where it was associated with PEG than where PEG was absent (202 vs 135 g; SEM = 17; $P = 0.022$). Groups did not differ in their intake of the tannin-containing food (group effect; $P = 0.117$) or in their pattern of food intake at locations with or without PEG (group × location; $P = 0.597$; group × location × period $P = 0.150$). Intake of the tannin food at the two locations was not influenced by period (location × period; $P = 0.226$).

Intake of PEG. Intake of PEG depended on the gradient of tannin concentrations ($P = 0.0001$). A preload of the tannin-containing food did not modify intake of PEG relative to the period without a preload of the tannin-containing food, but intake of PEG increased over two-fold when lambs were fed a basal diet of the tannin food ($P = 0.0001$; Figure 2). Intake of PEG did not differ between groups (group effect; $P = 0.665$) and groups did not differ in their intake of PEG across periods (group × period; $P = 0.677$).

Feeding Time. The presence of PEG influenced the time that lambs spent at each location (Figure 2). Averaged across periods, lambs spent more time at the side where PEG was present than at the side where PEG was absent and only the tannin-containing food was available (8.6 vs 4.7 min; SEM = 0.8; $P = 0.012$). Feeding time was influenced by the amount of tannins that lambs ingested before testing (location × period; $P = 0.072$; Figure 2). When the tannin-containing food was the basal diet, lambs spent more time at the location with PEG than when they did ($P = 0.0001$) or did not ($P = 0.0625$) have a preload of this food (Figure 2). Groups did not differ in their feeding time (group effect; $P = 0.117$) or in the time spent at locations with or without PEG (group × location; $P = 0.935$; group × location × period $P = 0.111$).

Trial 2: Preference for Locations with Tannins vs Locations with PEG

Intake of the Tannin-Containing Food. Group 1 consumed less tannin food than Group 2 (235 vs 326 g; SEM = 24; $P = 0.0311$), and the pattern of food consumption between groups differed across periods (group × period; $P = 0.060$). For lambs in Group 1, intake of the tannin food was higher in the period without a tannin preload than in the periods with a tannin preload and with a basal diet of the tannin food (329 vs 183 and 194 g; $P = 0.001$). For lambs in Group 2, intake of the tannin food decreased consistently from the period without a tannin preload to the period when the basal diet was the tannin food (432, 315, and 231 g, respectively; SEM = 29; $P = 0.001$). Thus, for both groups there was a decrease in consumption of the tannin-containing food as the amount of tannins ingested before testing increased (from no ingestion to a basal diet containing 15% tannins, period effect; $P = 0.0001$; Figure 3).

Intake of PEG. Intake of PEG was influenced by the amount of tannins ingested by lambs before testing (period, $P = 0.001$). Intake of PEG tended to increase from the period without a tannin preload to the period with a tannin preload ($P = 0.100$) and from the period with a tannin preload to the period when the tannin food was the basal diet ($P = 0.008$; Figure 3). Intake of PEG did not differ between groups (group effect; $P = 0.401$), and groups did not differ in their intake of PEG across periods (group × period; $P = 0.521$).

Feeding Time. Groups did not differ in their feeding time (group effect; $P = 0.2945$), but they differed in the amount of time they spent at locations with or without PEG (Group × location; $P = 0.0143$; group × location × period $P = 0.0168$). The presence of PEG and tannins influenced feeding time by both groups of lambs in a similar manner. From the period without a tannin pre-

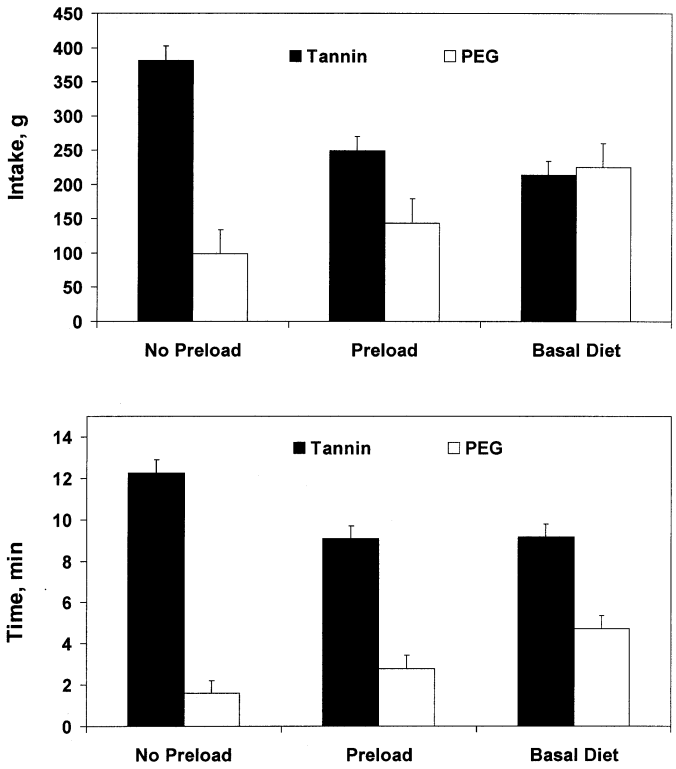

Figure 3. Intake (± SEM) of a food with 15% quebracho tannin and polyethylene glycol (PEG) at two different locations and time (± SEM) spent at those locations by two groups of lambs. Lambs could choose between a location that contained the tannin food (Tannin) and another location that contained PEG (PEG). Tests were conducted across a gradient of increased tannin concentrations in the lambs' diet (No preload; Preload: 1-h meal of the tannin food before testing; Basal Diet: The tannin food replaced a basal diet of alfalfa pellets).

load to the period when the tannin food was the basal diet, both groups of lambs increased the amount of time spent at the site with PEG (group 1: from 1.9 to 5.2 min.; group 2: from 1.2 to 4.1 min.; $P = 0.010$) and decreased the amount of time spent at the site with only the tannin-containing food (Group 1: from 11.5 to 8.4 min.; Group 2: from 13.0 to 9.9 min.; SEM = 0.9; $P = 0.010$). Lambs in Group 1 also spent more time at the location with PEG after a preload of the tannin-containing food than after no preload (3.9 vs 1.9 min; $P = 0.014$), but Group 2 did not (1.7 vs 1.2 min $P = 0.300$). In contrast, both groups of lambs spent less time at the location with the tannin-containing food after a preload of tannins than after no preload (Group 1: 6.3 vs 11.5 min.; $P = 0.010$; Group 2: 11.8 vs 13.0 min $P = 0.100$). Thus, in general, both groups of lambs increased the time spent at locations with PEG and decreased the time spent at locations with only the tannin food as the amount of tannins ingested before testing increased (location × period; $P = 0.0001$; Figure 3).

Discussion

Sheep learn to ingest substances that rectify maladies. For instance, sheep that overingest grain subsequently ingest sodium bicarbonate, which rectifies their acidotic condition (Phy and Provenza, 1998). Sheep fed diets high in tannins also ingest PEG, which binds to tannins (Provenza et al., 2000; Villalba and Provenza, 2001). Thus, we hypothesized that if sheep recognize the benefits of ingesting PEG when fed tannin-rich diets, then they should actively seek locations that contain PEG. Consistent with this, our results suggest that PEG influenced foraging location by sheep. Lambs spent more time and ate more of the tannin-containing food at locations where PEG was present than where it was absent (Figure 2).

Lambs eat PEG in amounts that are directly proportional to the tannin content of their diets (Provenza et al., 2000). Increased intake of PEG occurs during or after tannin consumption, but this effect disappears when tannins are absent from the diet (Provenza et al., 2000; Villalba and Provenza, 2001). This behavior seems to be PEG-specific, because it does not occur with control foods such as wheat straw that do not provide the "medicinal" effects of PEG (Villalba and Provenza, 2001). Lambs prefer PEG to wheat straw after eating quebracho tannin (Villalba and Provenza, 2001), which is consistent with the substantial increases in intake of foods containing quebracho tannin after supplementation with PEG (Provenza et al., 2000; Titus et al., 2000) relative to supplementation with wheat straw (Villalba and Provenza, 2001). Polyethylene glycol is a polymer that can bind several classes of tannins present in different plant species (Landau et al., 2000), including quebracho, the condensed tannin extracted from the South-American quebracho tree (*Aspidosperma quebracho*).

During conditioning with PEG, removal of barley, the nutritive component of the barley/PEG mixture, caused only a brief depression in intake of PEG (Figure 1), even though PEG does not have any nutritional value (Bauman et al., 1971). Thus, the sustained ingestion of PEG suggests lambs ate PEG due to its benefits at neutralizing tannins. Lambs spent significant amounts of time at locations where only PEG was available (Figure 3), which also implies animals consumed PEG as a consequence of its beneficial effects.

The beneficial effects of PEG at neutralizing tannins can also modify the pattern of herbivore selectivity in plant communities containing tannin-rich vegetation. For instance, goats supplemented with PEG increased intake of tannin-rich vegetation, and this pattern was not modified even when goats had alfalfa hay available while they foraged (Landau et al., 2002). Our study suggests that supplemental PEG may modify the distribution of livestock within tannin-dominated vegetation. In turn, the results of Landau et al. (2002) imply that PEG consumption can substantially modify foraging patterns across plant communities.

Lambs responded to increased loads of quebracho tannin by reducing both intake and the time allocated to sites containing only quebracho tannin and by increasing intake and preference for the sites containing PEG (Figures 2 and 3). These results are consistent with a decreased preference for tannins and an increased preference for PEG proportional to the amount of exposure to tannins (Provenza et al., 2000). As tannin ingestion increased across periods, satiation on the tannin-containing food likely encouraged lambs to explore alternative sites. In turn, foraging time and intake at sites containing PEG may have increased as a consequence of the beneficial effects of PEG on tannins (Villalba and Provenza, 2001).

In summary our results imply that PEG may be used to modify foraging distribution by herbivores fed tannin diets. Thus, besides water, supplement, salt, shade, and shelter (Bailey et al., 1998), the use of PEG may be an effective substance to attract livestock to underutilized feeding sites in plant communities dominated by species with high concentrations of tannins.

Implications

The high content of condensed tannins in some plants substantially diminishes their forage value even for tolerant animal species such as goats. Polyethylene glycol (PEG) can increase intake of tannin-containing plants, thereby enhancing animal performance. However, providing supplemental PEG can be labor-intensive under extensive conditions, such as rangelands where livestock are distributed over large areas. Our results imply it may be possible to formulate range blocks that allow herbivores to ingest PEG in a tannin-dominated vegetation and suggest that strategic distribution of PEG may attract herbivores to underutilized feeding sites.

Literature Cited

Bailey, D. W., B. Dumont, and M. F. WallisDe Vries. 1998. Utilization of heterogeneous grasslands by domestic herbivores; Theory to management. Ann. Zootech. 47:321–333.

Bauman, D. E., C. L. Davis, R. A. Frobish, and D. S. Sachan. 1971. Evaluation of polyethylene glycol method in determining rumen fluid volume in dairy cows fed different diets. J. Dairy Sci. 54:928–930.

Dawson, J. M., P. J. Buttery, D. Jenkins, C. D. Wood and M. Gill. 1999. Effects of dietary quebracho tannin on nutrient utilization and tissue metabolism in sheep and rats. J. Sci. Food. Agric. 79:1423–1430.

Foley, W. J., G. R. Iason, and C. McArthur. 1999. Role of plant secondary metabolites in the nutritional ecology of mammalian herbivores: How far have we come in 25 years? in: H. G. Jung and G. C. Fahey, Jr. (ed.) Nutritional Ecology of Herbivores. In: Proc. 5th Int. Symp. Nutr. Herb. pp 130–209. Am. Soc. Anim. Sci., Savoy, IL.

Hagerman, A. E., C. T. Robbins, Y. Weerssuriya, T. C. Wilson and C. McArthur. 1992. Tannin chemistry in relation to digestion. J. Range Manage. 45:57–62.

Jones, W. T., and J. L. Mangan. 1977. Complexes of condensed tannins of sainfoin (*Onobrychis viciifolia Scop.*) with fraction-1 leaf protein and with submaxillary mucoprotein, and their reversal by polyethylene-glycol and pH. J. Sci. Food Agric. 28:126–136.

Landau, S., A. Perevolotsky, D. Bonfil, D. Barkai, and N. Silanikove. 2000. Utilization of low quality resources by small ruminants in Mediterranean agro-pastoral systems: the case of browse and aftermath cereal stubble. Livest. Prod. Sci. 64:39–49.

Landau, S., A. Perevolotsky, D. Kabaya, N. Silanikove, R. Nitzan, H. Baram, and F. D. Provenza. 2002. Free intake of polyethylene-glycol modifies the behavior of goats feeding on tannin-rich Mediterranean shrubland. J. Range. Manage. (In press).

Littell, R. C., Milliken, G. A., Stroup, W. A., and Wolfinger, R. D. 1996. Statistical Analysis Systems for Mixed Models. SAS Institute, Cary, NC.

Phy, T. S., and F. D. Provenza. 1998. Sheep fed grain prefer foods and solutions that attenuate acidosis. J. Anim. Sci. 76:954–960.

Provenza, F. D., E. A. Burritt, A. Perevolotsky, and N. Silanikove. 2000. Self-regulation of intake of polyethylene glycol by sheep fed diets varying in tannin concentrations. J. Anim. Sci. 78:1206–1212.

Provenza, F. D., J. J. Villalba, C. D. Cheney, and S. J. Werner. 1998. Self-organization of foraging behavior: From simplicity to complexity without goals. Nut. Res. Rev. 11:199–222.

Silanikove, N., D. Shinder, N. Gilboa, M. Eyal, and Z. Nitsan. 1996. Binding of poly (ethylene glycol) to samples of forage plants as an assay of tannins and their negative effects on ruminal degradation. J. Agric. Food Chem. 44:3230–3234.

Titus, C. H., F. D. Provenza, A. Perevolotsky, and N. Silanikove. 2000. Preferences for foods varying in macronutrients and tannins by lambs supplemented with polyethylene glycol. J. Anim. Sci. 78:1443–1449.

Villalba, J. J., and F. D. Provenza. 2001. Preference for polyethylene glycol by sheep fed a quebracho tannin diet. J. Anim. Sci. 79:2066–2074.