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Sagebrush ingestion by lambs: Effects of experience and macronutrients

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Abstract

We investigated how experience early in life and macronutrient content of the diet influenced intake of mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) by sheep. In the first part of our study, 2-month-old lambs were exposed as a group for 2 mo to a 70% barley-30% soybean meal ration (300 g/hd/day) that contained increasing amounts sagebrush (1 to 20%). Control lambs received grain without sagebrush. All lambs had access to alfalfa hay and pellets ad libitum. When lambs were tested at 6 months of age, prior exposure had no effect on sagebrush consumption after the first 4 days of the trial. When sagebrush comprised 20% of an alfalfa/barley ration, lambs ate the sagebrush ration readily even when a nutritious alternative was offered indicating the flavor of sagebrush did not prevent lambs from feeding. Increasing the amount of sagebrush in the ration from 50% to 75% resulted in lambs eating less of the barley/sagebrush ration, but daily intake of sagebrush remained constant throughout the 4 day trial, presumably because toxins (terpenes) limited intake of sagebrush. In the second part of our study, lambs experienced with sagebrush were fed 250 g/hd/day of barley, and nutritional status was varied by offering alfalfa pellets at 33% or 80% of ad libitum (1.2 and 2.7 times maintenance, respectively) to determine if dietary energy levels affected intake of sagebrush. Each day lambs received a 50/50 sagebrush/barley supplement ad libitum for 1 hour. Lambs fed at 33% of ad libitum consumed more of the sagebrush/barley supplement than lambs fed at 80% of ad libitum. Thus, additional energy did not enable lambs to consume more sagebrush. In the last trial, lambs in both treatments were fed a basal ration of alfalfa pellets at 50% of ad libitum. Each morning for 1 hour, lambs were offered macronutrient supplements containing either 50% barley/50% sagebrush (high energy) or 25% barley/25% soybean meal/50% sagebrush (high energy and protein). Lambs consumed the same amount of sagebrush regardless of supplement. Thus, supplemental protein did not improve sagebrush consumption. We conclude lambs readily ingested a high-energy ration containing sagebrush, regardless of exposure early in life, suggesting toxins, not flavor, control intake of sagebrush. Further, supplementing lambs with energy or protein failed to improve intake of sagebrush, which suggests these macronutrients did not enhance detoxification of sagebrush.

Key Words: ***Artemisia tridentata*, sheep, toxins, intake, terpenes, diets**

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Resumen

Investigamos como la experiencia adquirida a temprana edad y el contenido de micronutrientes de la dieta influye en le consumo de "Mountain big sagebrush" (*Artemisa tridentata* Nutt. *vayesana* (Rydb.) Beetle) por ovinos. En la primer parte de nuestro estudio, corderos de 2 meses de edad se expusieron como grupo durante 2 meses a una ración de 70% cebada – 30% soya (300 g/cabeza/día) que contenía cantidades crecientes de "sagebrush" (1 a 20%). Los corderos del tratamiento control recibieron grano sin "sagebrush". Todos los corderos tenían libre acceso a heno y pelets de alfalfa. Cuando los corderos fueron evaluados a los 6 meses de edad. la exposición previa no tuvo efecto en el consumo de "sagebrush" después de los primeros 4 días del ensayo. Cuando el "Sagebrush" constituyó el 20% de la ración alfalfa/cebada, los corderos comieron fácilmente la ración de "Sagebrush", aun cuando se ofrecieron alternativas nutritivas, lo que indica que el sabor del "Sagebrush" no evita que los corderos se alimenten. El aumento de la cantidad de "Sagebrush" en la ración de 50% a 75% resultó en que los corderos comieron menos de la ración alfalfa/cebada, pero el consumo diario de "Sagebrush" permaneció constante hasta el cuarto día del estudio, presumiblemente porque las toxinas (terpenos), limitaron el consumo de "Sagebrush". En la segunda parte de nuestro estudio, los corderos que experimentaron con "Sagebrush" fueron alimentados con 250 g/cabeza/día de cebada, y el estado nutricional se varió ofreciendo pelets de alfalfa a un 33% o 80% del consumo libre (1.2 y 2.7 veces el mantenimiento respectivamente) para determinar si los niveles de energía dietaria afectaron el consumo de "Sagebrush". Cada día los corderos recibieron, a libre acceso durante una hora, un suplemento de 50/50 de "Sagebrush"/cebada. Los corderos alimentados con un 33% del consumo libre comieron mas del suplemento "Sagebrush/"cebada que los corderos alimentados al 80% del consumo libre. Así, la energía adicional no induce a los corderos a comer mas "Sagebrush". En el ultimo ensayo, los corderos en ambos tratamientos se alimentaron con una ración basal de pelets de alfalfa al 50% del consumo libre. Cada mañana, durante una hora. se les ofreció a los corderos suplementos de micronutrientes conteniendo 50% cebada / 50% "Sagebrush" (alta energía) o 25% cebada / 25% soya / 50% "Sagebrush" (alta energía y proteína). Los corderos consumieron la misma cantidad de "Sagebrush " independientemente del suplemento. Como resultado, la suplementación protéica no mejoro el consumo de "Sagebrush". Concluimos que los corderos consumieron fácilmente una ración alta en energía que contenia "Sagebrush, esto sin importar la exposición al "sagebrush" al que se sometieron a la edad temprana, sugiriendo que las toxinas, y no el sabor, controlan el consumo de "sagebrush. Además, el suplementar los corderos con energía y proteína fracasó en mejorar el consumo de "sagebrush", lo que sugiere que estos micronutrientes no aumentan la detoxificacion de ‘sagebrush"

Sagebrush (*Artemisia tridentata* ssp.) is a dominant species on millions of hectares of rangeland in the western United States. As a forage, it generally is not preferred by either sheep or cattle, especially during the growing season. Low use of sagebrush is often attributed to its monoterpenoid content (Yabann et al. 1986). Terpenoids depress in vitro digestion of sagebrush (Striby et al. 1987) and wethers fed grass/sagebrush diets exhibit marked depression in in vivo digestibility (Ngugi et al. 1995). Sagebrush can also be lethal to sheep (Johnson et al. 1976).

Exposure to sagebrush early in life may increase preference for sagebrush. Sheep with experience eating sagebrush consume more of the shrub than inexperienced sheep when alternative forages are lacking (Narjisse 1981). The degree to which exposure can increase a food's acceptability depends on the food's toxicological and nutritional properties. It is unlikely that herbivores can ever be conditioned to consume large amounts of foods high in toxins (Distel and Provenza 1991) because toxins set a limit on the amount of nutritious foods herbivores can ingest (Wang and Provenza 1997). On the other hand, exposure early in life can enhance preference for foods that are low (Distel and Provenza 1991) or high (Villalba and Provenza 1997a) in macronutrients, provided foods are not toxic.

An animal's nutritional state may also affect its ability to consume plants such as sagebrush that contain toxins (terpenes). Toxins are absorbed, biotransformed and metabolized by mammals to form organic acids that must be buffered and excreted from the body (Foley et al. 1995, McArthur et al. 1991). Illius and Jessop (1995) propose detoxification requires additional expenditures of amino acids and glucose to conjugate with toxins and maintain an animal's acid-base balance. Thus, a diet low in energy and protein may provide inadequate levels of substrate for terpene detoxification and limit the amount of sagebrush animals can eat.

Our objectives were to investigate how experience early in life and macronutrient content of the diet influenced intake of sagebrush by sheep. In the first study, we hypothesized lambs exposed to sagebrush early in life would have a higher preference for sagebrush later in life than lambs without exposure to sagebrush. In the second experiment, we speculated lambs consuming more macronutrients would have more nutrients available to detoxify terpenes and would consume more sagebrush than lambs on a poorer nutritional plane.

Materials and Methods

Sagebrush

We conducted 5 trials. Sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) used in Trials 1, 2 and 3 was vegetative growth with a maximum twig size of 3.5 mm and was hand-harvested from 22 March to 15 April 1996 approximately one-half mile southeast of Paradise, Utah. Sagebrush was placed in the freezer within 2 hours of collection; several days later the frozen sagebrush was passed through a garden chipper-shredder (chipped to 1–2 cm lengths) and immediately returned to the freezer until thawed and fed. Sagebrush contained about 50% moisture. Sagebrush used in Trials 4 and 5 was vegetative and reproductive growth with a maximum twig size of 3.5 mm, collected during September at the Green Canyon Ecology Center, North Logan, Utah. It was hand-harvested each morning and immediately passed through a garden chipper-shredder, mixed with ground food and fed fresh.

Sheep

Lambs used in Trials 1, 2, and 3 were orphans (crossbred Suffolk), reared on milk replacer until 4 weeks of age. At weaning they were offered free choice a soybean meal/corn/barley ration, alfalfa hay and pellets. When lambs were 2-months-old they were weighed and randomly assigned (by weight) to 2 treatments and placed in 2 separate pens. For 2 months, half of the lambs (n=12) received sagebrush in their grain ration (70% barley, 30% soybean meal, 300 g/hd/day of the sagebrush/barley/soybean meal ration). The amount of sagebrush in the ration was initially 1% and was increased 1% every 5 days until it reached 4%, then increased 4% every 5 days until it reached 20%; the amount of sagebrush in the ration remained at 20% for 25 days. The other group of lambs (n=12) received the same foods without sagebrush. In addition to the grain ration, lambs also had access to alfalfa pellets and alfalfa hay ad libitum. Following the 60-day exposure, all lambs grazed a common grass pasture for 2 months. When lambs were 6-months-old, they were placed in individual pens so we could measure intake of sagebrush. Throughout the trials, lambs had access to trace mineralized salt blocks and water ad libitum.

Lambs used in Trials 4 and 5 were 3-mo-old wethers (white-faced commercial crossbred lambs). They were reared on alfalfa hay and pellets and weaned at 60 days of age. Lambs were placed in individual pens prior to the onset of the trials. They were exposed to increasing levels of sagebrush (10% to 50%) mixed with ground alfalfa for 1 hour each day for 30 days. They had access to water and mineral blocks ad libitum during conditioning and trials.

Exposure early in life

Trial 1

The objective of Trial 1 was to determine if lambs exposed to sagebrush early in life had a higher preference for a sagebrush ration than control lambs (naive to sagebrush). In this trial, the sagebrush ration contained 15% more energy than the alternative ration (2.3 vs. 2.0 Mcal ME/kg dry matter basis (dmb)(NRC 1985)). Each morning at 0900 hours lambs were offered a choice between a mixture of 50% ground alfalfa/30% ground barley/20% ground sagebrush and 100% ground alfalfa. Food refusals were collected and weighed at the end of an hour and intake calculated on an as-fed basis. Lambs had access to alfalfa pellets ad libitum until 1700 hours, when food boxes were removed and emptied. The trial lasted 5 days. Lambs received 200 g of each food on day 1, 250 g of each food on day 2, and they had ad libitum access to each food on days 3–5. On days 1 and 2 of the trial, food boxes were removed before the end of the hour, if lambs consumed all of 1 of the 2 foods offered.

Trial 2

The objective of Trial 2 was to determine if lambs with early exposure to sagebrush would consume more sagebrush than control lambs when the 2 rations offered had similar energy contents (2.3 Mcal ME/kg dmb (NRC 1985)). In other words, would lambs continue to eat the sagebrush ration if it no longer contained more energy than the alternative ration? Each morning at 0900 hours lambs were offered a choice of a mixture of 70% ground alfalfa/30% ground barley and a mixture of 50% ground alfalfa/30% ground barley/20% ground sagebrush for 1 hour. During the trial, foods were offered ad libitum. Food refusals were collected and weighed at the end of the hour and intake calculated on an as-fed basis. Lambs then received alfalfa pellets ad libitum until 1700 hours when food boxes were removed and emptied. The trial lasted 4 days.

In Trials 1 and 2 intake was calculated on a dry matter basis and expressed as percent sagebrush-ration in the diet. When the percent of sagebrush-ration in the diet was above 50% it was preferred and below 50% it was avoided.

Trial 3

The objective of Trial 3 was to determine if lambs exposed to sagebrush early in life consumed more sagebrush than lambs naive to sagebrush when no alternative food was available. Each morning at 0900 hours lambs had ad libitum access to a mixture of 50% sagebrush/50% ground barley for 1 hour. Food refusals were collected and weighed at the end of 1 hour and intake calculated on an as-fed basis. Lambs then received alfalfa pellets ad libitum until 1700 hours when food boxes were removed and emptied. The trial lasted 4 days. Finally, sagebrush concentration was increased to 75% and lambs had ad libitum access to the ration for 1 hour/day for 2 days more.

Nutritional state

Trial 4

The objective of Trial 4 was to determine if lambs' macronutrient status affected sagebrush consumption. Lambs (n=12/treatment) were offered a basal ration of 250 g of barley, and nutritional status was varied by offering alfalfa pellets at either 33% or 80% of ad libitum intake (1.2 and 2.7 times NE_m, respectively). Levels of intake (33% and 80% of ad libitum) were chosen so we could compare our results to those of Wang and Provenza (1996). To determine ad libitum intake, lambs were offered 250 g of ground barley each morning followed by alfalfa pellets for 24 hour/day for 4 days and intake was recorded each day. Barley was fed prior to offering alfalfa pellets because a barley/sagebrush ration was to be fed to lambs during the subsequent trial, and we estimated lambs would consume about 250 g of a 50/50 sagebrush/barley ration in 1 hour based on earlier feeding trials. Lambs were ranked by level of intake and assigned to the 2 treatments alternatively from highest to lowest intake. Lambs were fed treatment rations for 2 days before the onset of the trial and throughout the 5-day trial. Each morning during the trial, lambs were offered a 50/50 mix of ground barley and sagebrush (2.6 Mcal ME/kg; 12% CP dmb (NRC 1985)) ad libitum from 0800 to 0900 hours. On days when lambs ate less than 250 g of the sagebrush/grain mix, we provided additional barley to ensure that all lambs received the same amount of macronutrients from their supplement each day. Lambs then received alfalfa pellets.

Trial 5

The objective of Trial 5 was to determine if lambs consuming adequate levels of protein for maintenance and growth consumed more sagebrush if they were offered additional dietary protein. All lambs were fed alfalfa pellets at 50% ad libitum prior to (2 days) and during (5 days) the trial. Lambs received either a 50/50 mixture of barley and sagebrush (2.6 Mcal ME/kg and 12% CP dmb (NRC 1985)), or a 25/25/50 mixture of soybean meal, barley and sagebrush (2.7 Mcal ME/kg and 24% CP dmb (NRC 1985)). Each morning lambs received the sagebrush/concentrate supplement ad libitum for 1 hour. Lambs then received alfalfa pellets. Assignment to treatments in Trial 5 was such that lambs from different treatments in Trial 4 occurred equally in both treatments in Trial 5.

Statistical analyses

To test if exposure early in life affected intake of sagebrush in Trials 1, 2 and 3, we used a repeated measures analysis of variance with 2 treatments (early-exposure to sagebrush and control); lambs (n=12) nested within treatments was the error term to test differences between treatments. Day was the repeated measure. Several additional analyses of variance were also conducted; for control lambs in Trial 1 and all lambs in Trial 2, we tested if intake of the ration with sagebrush differed from intake of the ration without sagebrush. There were 2 treatments (sagebrush vs. no sagebrush) and lambs crossed with treatments was the error term. Day was the repeated measure. For Trial 3, two additional analyses were run to test the effect of increasing the proportion of sagebrush in the ration on intake of the sagebrush/barley ration and on sagebrush alone. Data from days 1 and 2 of the trial were omitted from these analyses so that we had an equal number of days when sagebrush was fed as 50% and 75% of the ration (2 days at each level). In both analyses day (n=4, 2 days at 50% and 2 days at 75% sagebrush) was the treatment and lambs (n=24) crossed with day was the error term to test for differences between days. In Trials 4 and 5, the repeated measure analysis of variance had 2 treatments (Trial 4–33% and 80% ad libitum; Trial 5 –soybean meal and no soybean meal) and lambs nested within treatments was the error term to test differences between treatment means. Day was the repeated measure. For all analyses, when F-ratios for main effects and interactions were significant ($P<0.05$), multiple mean comparisons using LSD were used to test differences among treatment means.

Results

Exposure early in life

During Trial 1, lambs with early exposure to sagebrush and control lambs were offered 2 rations, one with and the other without sagebrush (the sagebrush ration contained 15% more energy). Lambs with early exposure to sagebrush had a higher preference for the sagebrush/barley/alfalfa ration compared with control lambs, but the differences between treatments persisted only for the first 4 days of the trial (trt x day interaction $P<0.001$; Fig. 1). Lambs with early exposure to sagebrush consumed the same amount of each ration regardless of sagebrush content (144 g/hd/day for both rations, SEM=12, P=.96).

During Trial 2, when lambs were offered 2 rations equal in energy, 1 with sagebrush and 1 without sagebrush, lambs did not differ in their preference for the sagebrush ration (45% control vs 42% early exposure, SEM=2.2, P=0.41). Regardless of prior experience, lambs preferred the ration without sagebrush to the ration with sagebrush (207 g vs. 153 g, respectively, SEM=7.0, $P<0.001$).

During Trial 3, when lambs were offered only 1 ration (either 50/50 or 75/25 sagebrush/barley), lambs with early exposure to sagebrush and control lambs

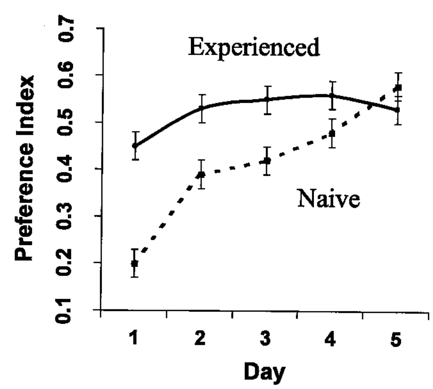

Fig. 1. Percent of a 20/30/50 sagebrush/barley/alfalfa ration in the total diet consumed by lambs with and without prior exposure to sagebrush. The alternative food offered during Trial 1 was 100% ground alfalfa. Bars represent standard errors of the mean. $LSD_{.05}$ = 6.1.

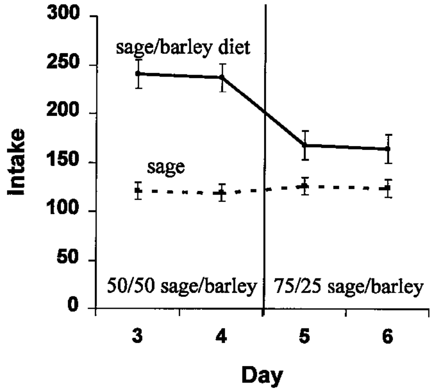

Fig. 2. Intake by all lambs fed a 50/50 sagebrush/barley ration (days 3 and 4) and a 75/25 sagebrush/barley ration (days 5 and 6). Solid line is intake of the sage/barley rations; dashed line is intake of sagebrush in those rations. Comparisons between means are made across days. Bars represent standard errors of the mean. $LSD_{.05}$ = 29 for the sagebrush/barley diets.

ingested similar amounts of sagebrush (126 g control vs. 117 g early exposure, SEM = 11.0, P=0.57). When the amount of sagebrush in the sagebrush/barley ration was increased from 50% to 75%, lambs ingested less of the 75% sagebrush/25% barley ration than the 50/50 ration, but total daily sagebrush intake remained constant throughout the 4-day trial (Fig. 2).

Individual lambs varied in their consumption of sagebrush. Some lambs ingested as little as 60 g/hour, whereas others consistently ate as much as 180 g/hour (SEM=8.9).

Nutritional state

In Trial 4, lambs that received a basal ration of 33% ad libitum consumed more of the sagebrush/barley ration than lambs that received 80% of ad libitum intake (205 g vs. 151 g respectively; P=0.056). The difference became more pronounced as the trial progressed (trt x day interaction P=0.008; Fig. 3). In Trial 5, lambs that received the soybean meal/barley/sagebrush ration and lambs that received the barley/sagebrush ration consumed similar amounts of the grain/sagebrush mixtures throughout the 5-day trial (soybean meal= 251 g; no soybean meal=256 g; SEM=21.5, P=0.86).

Discussion

Exposure early in life

Lambs with prior exposure to sagebrush did not eat more sagebrush than control lambs except during the first 4 days of Trial 1. The gradual increase in intake of the sagebrush ration by control lambs is comparable to the intake pattern of lambs introduced to any (non-toxic nutritious) novel food or flavor (Provenza et al. 1995). In Trial 2, lambs ate sagebrush readily regardless of prior exposure, even when a nutritious alternative was available. In other studies, experience with sagebrush did not increase sagebrush intake by mature sheep (Narjisse 1981) or goats (Richman et al. 1994) when alternative forages were available. In Trial 3, prior exposure continued to have no effect on intake when a sagebrush/barley ration was the only food available. Narjisse (1981) observed that sheep experienced with sagebrush only consumed more sagebrush than naive sheep when alternative foods were limited. However, Pritz et al. (1997) observed a slight decrease in intake of redberry juniper by goats given juniper essential oils early in life.

During Trial 3, lambs in both groups consumed more of the barley/sagebrush ration containing 50% sagebrush than the ration containing 75% sagebrush, but they ate the same amount of sagebrush regardless of the amount of barley mixed with sagebrush. These findings suggest toxic compounds in sagebrush limited the amount of sagebrush lambs could consume. Sagebrush contains a diverse array of terpenes (Kelsey et al. 1982, Bray et al. 1991) that are potentially toxic (Johnson et al. 1976). Thus, we hypothesize terpenes set a limit on the amount of food lambs consumed (i.e., toxin satiation). This hypothesis is consistent with the observation that lambs eating sagebrush/grass diets limited terpenoid ingestion to 170 mg/kg metabolic weight/day (Ngugi et al. 1995) and that toxins can limit the amount of foods lambs can ingest (Launchbaugh et al. 1993, Wang and Provenza 1997).

In our study, experienced lambs did not eat more sagebrush than inexperienced lambs, but the reverse was true in other studies with goats (Distel and Provenza 1991) and sheep (Distel et al. 1996). The nutrient and toxin content of the food likely determines whether exposure early in life will increase preference. If a food is low in macronutrients, but not toxic, then exposure early in life can increase preference by causing various neurological, morphological and physiological changes in animals (Distel et al. 1994, 1996). On the other hand, if a food is toxic, no amount of exposure is likely to increase intake beyond the level of toxin satiation (Distel and Provenza 1991), unless exposure enhances detoxification. Exposure can decrease the lethal effects of a toxin (Cheeke and Shull 1985, Johnson et al. 1976) by improving a ruminant's ability to detoxify a compound (Frutos et al. 1999), but it is not clear whether these adaptations always lead to an increase in intake of a toxic food. For example, Frutos et al. (1999) reported that goats adapted to oxalate, detoxified oxalate to a greater extent than non-adapted goats, but adapted goats did not eat more of an oxalate-containing diet than non-adapted goats. Our data suggest that toxins (terpenes) limit intake of sagebrush by lambs and early exposure is not likely to enhance sagebrush consumption beyond the limit of toxin satiation.

Our data suggest that the flavor of sagebrush had little effect on the consumption of sagebrush by lambs. Experienced lambs in Trial 1 ate the same amount of each ration regardless of sagebrush content. When the ration containing sagebrush and the alternative ration had similar energy contents (Trial 2), both groups of lambs showed only a modest preference for the diet without sagebrush. Evidently, the flavor of sagebrush did not prevent lambs from eating the ration containing sagebrush because lambs consumed both rations instead of solely eating the ration without sagebrush.

Nutritional state

Illius and Jessop (1995) hypothesize that animals limit consumption of toxins when nutritional stress reduces their tolerance to allelochemicals. According to their mathematical model, animals that consume energy at twice maintenance should be able to

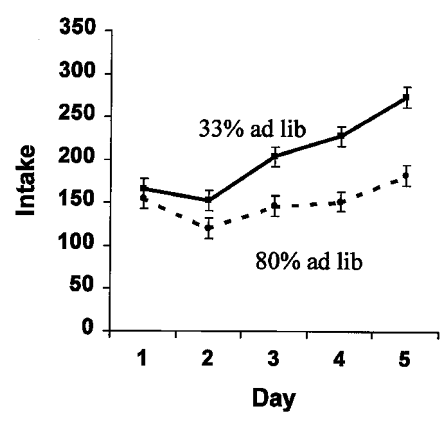

Fig. 3. Consumption of a 50/50 sagebrush/barley ration by lambs maintained at either 33% or 80% ad libitum. Bars represent standard errors of the mean. $LSD_{.05}$ = 23.

tolerate the maximum concentration of allelochemicals.

Wang and Provenza (1996) reported energy affected the amount of lithium chloride (LiCl) lambs could ingest. Lambs fed a barley-based ration at 1/3 ad libitum ingested less LiCl than lambs fed at 2/3 ad libitum or ad libitum. They speculated lambs on restricted rations may limit intake of LiCl because it causes hypoglycemia, which is attenuated by energy in supplemental barley. In contrast, lambs in our study (Trial 4) fed at 33% ad libitum (1.2 times maintenance) ate more sagebrush than lambs fed at 80% ad libitum (2.7 times maintenance). Thus, our results are not consistent with the hypothesis animals consuming more energy in their basal ration ingest more toxins, evidently because lambs fed at 33% ad libitum had a greater need for nutrients that was not offset by aversive effects of terpenes. Our results differ from those of Wang and Provenza (1996), perhaps because LiCl and terpenes have different physiological effects. Lambs in their study also could consume foods with or without LiCl, whereas in our study lambs could either eat a supplement containing sagebrush or not eat.

The source of the energy and when it is ingested in relation to sagebrush consumption may also have an impact on intake of sagebrush. Banner et al. (1999) found that lambs fed barley immediately prior to eating sagebrush ate more sagebrush than lambs fed no barley. In our study, barley was mixed with sagebrush so lambs in both groups ate a readily fermentable source of energy with sagebrush. Banner et al. (1999) also found, as we did, that lambs fed an adequate basal ration - and a high-energy supplement - did not eat nearly as much sagebrush as food-deprived lambs fed the same high-energy supplement. Collectively, these data suggest that intake of sagebrush is likely to be highest when lambs are concurrently supplemented with a readily available source of energy and when lambs are somewhat food deprived.

The deterrent nature of allelochemicals may also be caused by the body's increased demand for nitrogen and amino acids during allelochemical detoxification; thus, increasing protein ingestion may increase allelochemical consumption (Illius and Jessop 1995). All lambs in Trial 5 received adequate protein for maintenance and growth (181 g/day, the requirement is 185 g/day for a 40 kg lamb gaining 275 g/day (NRC 1985)) from their basal ration of alfalfa pellets. Lambs fed the barley/soybean meal/sagebrush ration consumed twice as much additional protein (42 g) from their supplement as lambs fed the barley/sagebrush ration (21 g). Illius and Jessop (1995) predict animals may consume a food high in toxins if it provides sufficient nutrients for detoxification. They further speculate when animals consume protein over their requirement for net protein synthesis, the excess amino acids can be used for synthesis of glucose, which can be used for conjugation with toxins. In our study, increasing the amount of dietary protein in the supplement did not affect the amount of sagebrush consumed by lambs.

Foley et al. (1995) propose ingestion of forages high in secondary metabolites leads to increases in acidemia when their capacity to biotransform and eliminate secondary metabolites is exceeded. They speculate when this system is exceeded, postingestive feedback causes mammals to decrease intake of forages high in secondary metabolites. To date no feedback signal has been found from the biotransformation system that regulates intake. Another possibility is that the toxins in sagebrush stimulate the emetic system after the onset of eating and quickly cause a decrease in preference for sagebrush (Provenza 1995). Such an immediate response to toxins may be necessary to prevent animals from overingesting toxins (Provenza et al. 1994).

Sagebrush may also limit intake because terpenes are toxic to rumen microbes (Nagy et al. 1964, Oh et al. 1968). Animals forced to eat a ration of 30% sagebrush show marked depression in in vivo dry matter digestibility (Ngugi et al. 1995). Reduced microbial activity decreases digestibility of macronutrients and byproducts of fermentation (i.e., volatile fatty acids), all of which affect food preferences of sheep (Villalba and Provenza 1996, 1997a, 1997b, 1997c).

Conclusions

Some species (as well as subspecies and ecotypes) of sagebrush are more palatable to than others to sheep and mule deer, evidently because of differences in concentrations of terpenes (Welch et al. 1983, 1987, Personius et al. 1987). Neither exposure early in life, nor supplemental energy or protein caused a greater intake of sagebrush by lambs. The flavor of sagebrush did not prevent lambs from eating rations that contained sagebrush. Sagebrush intake was highly variable for individual lambs. Terpene levels in sagebrush vary seasonally (Kelsey et al. 1982), and sheep are most likely to use sagebrush when terpene concentrations are low and alternative forages are scarce (e.g. winter; Gade and Provenza 1986). Increasing use of sagebrush by livestock beyond the level of toxin satiation is unlikely unless the toxic compounds in sagebrush can be rendered inactive.

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