Rumen distension and contraction influence feed preference by sheep

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ABSTRACT: Distension of the rumen limits feed intake by livestock. Ruminal dysfunctions due to bloat, which causes distension by accumulation of excessive gas within the rumen, also reduce feeding. We hypothesized that excessive levels of rumen distension cause feed aversions and that preference increases for feeds eaten in association with recovery from bloat. To test these hypotheses, we determined whether 12 commercial crossbred lambs (average initial BW of 43 ± 2 kg) could associate ingestion of specific feeds with the consequences of increased intraruminal pressure and its subsidence. Six of the lambs were fitted with rumen cannulas and offered ground alfalfa for 30 min after a rubber balloon was inserted into the rumen of each animal and distended with air to volumes of 1.8, 2.5, or 4.5 L. Subsequently, balloons were deflated and alfalfa was offered again for a second period of 30 min. Feed intake was not affected when the balloon was not distended (P = 0.45 to 0.93), but distension reduced feed intake (P < 0.001) in direct proportion to the magnitude of distension at all 3 volumes (R² = 0.70). Relief from distension promoted a compensatory increase in feed intake (P = 0.006). During conditioning to determine if lambs acquired a preference for a feed associated with recovery from distension, fistulated lambs were offered novel feeds: wheat bran (group 1; n = 3) and beet pulp (group 2; n = 3), and the balloon was distended for 30 min. Feeds were then switched and the balloons were deflated (recovery). Control lambs (n = 6) received the same feeding protocol without the balloons. Lambs formed strong aversions to feeds associated with distension and preferred feeds associated with recovery (P = 0.001 to P = 0.10). No preferences or avoidances were observed in control lambs conditioned without rumen distension (P = 0.17 to P = 0.87). Thus, rumen distension and recovery from distension induced feed aversions and preferences, respectively, which may be critical in learning avoidance of bloat-inducing plants and preferences for plants and supplements that relieve the incidence of bloat.

Key words: bloat, diet selection, foraging, learning, sheep

INTRODUCTION

Bloat is a major nonpathogenic disease in livestock worldwide. It is characterized by an accumulation of fermentation gas within the rumen in sufficient quantity that normal intraruminal pressure is exceeded and distension occurs (Lippke et al., 1972; Essig et al., 1988).

Rumen distension and tactile inputs are important signals of satiety in livestock (Della Fera et al., 1990; Anil et al., 1993). Stretch receptors in the rumen or reticulum may monitor the level of distension and signal satiety once a threshold in distension has occurred (Grovum, 1979). Rumen distension may also be aversive and, as a consequence, induce satiety. The satiety hypothesis attributes changes in feed preference and intake to transient feed aversions as a result of sensory input (e.g., flavor of a feed) and postigestive effects (e.g., stimulation of chemo-, osmo-, and mechanoreceptors) unique to each feed (Provenza, 1995, 1996; Provenza and Villalba, 2006). Thus, under the satiety hypothesis, bloat-inducing feeds can be aversive. In contrast, feeds that contribute to the relief of aversive states (e.g., medicines) are preferred by ruminants (Villalba et al., 2006). Ruminants experiencing rumen distension may form preferences for feeds associated with recovery from distension. Tannin-containing feeds have the potential to reduce the incidence of bloat (Min et al., 2005), such that bloated animals may then increase preferences for bloat-relieving feeds.

The objectives of the present study were to determine whether sheep 1) reduce feed intake when they...
experience ruminal distension, 2) form aversions to feeds associated with distension of the rumen, and 3) form preferences for feeds associated with relief from increased intraruminal pressure.

MATERIALS AND METHODS

The study was conducted at the Green Canyon Ecology Center, located at Utah State University in Logan, according to procedures approved by the Utah State University Institutional Animal Care and Use Committee.

Animals

During the study, 12 commercial crossbred lambs (6 mo of age) with an average initial BW of 43 ± 2 kg were penned outdoors under a protective roof in individual, adjacent pens measuring 2.4 × 3.6 m. Six of the lambs were fitted with rumen cannulas (35 mm i.d., model 6C, Bar Diamond, Parma, ID). Lambs had free access to fresh water and trace mineral salt blocks. Before the study, lambs were given an adjustment period of 22 d in their individual pens, during which they received alfalfa pellets (initial 10 d) and ground alfalfa hay (final 12 d) during the same time intervals as during the experiment.

Distension of the Rumen

We hypothesized that rumen distension is aversive, promoting a reduction in feed intake and an aversion to the feeds associated with distension. In this experiment we determined whether distension of the rumen depresses feed intake as a function of the magnitude of the distension.

Intake Without a Balloon

To assess baseline intakes without the balloon, the 6 fistulated lambs were offered 1,600 g of ground alfalfa hay for 30 min at 0900 h. Refusals were collected and weighed, and alfalfa was offered again for a second period of 30 min (Table 1). Refusals were collected and weighed. Alfalfa was offered again until 1700 h, when refusals were collected and weighed and no other feed was offered until the next day.

Intake With a Balloon Without Distension

To determine if a nondistended balloon affected intake, a feeding procedure similar to that described in the previous section was used except that the balloon was inflated with air and then lambs were fed ground alfalfa for a period of 30 min. After collecting refusals for the first period of 30 min, balloons were completely deflated and alfalfa was offered again for a second period of 30 min (Table 1). After collecting refusals, balloons were removed and alfalfa was offered again until 1700 h, when refusals were collected; no other feed was offered until the next day.

Magnitude of Distension

Balloons were spherical in shape and before introducing them into the rumen, they were inflated and their circumference was used to estimate the resultant volume: \(4/3 \pi (C/2\pi)^3\), where \(C\) = circumference.

Feed intake was assessed with 3 different magnitudes of distension: 1.8, 2.5, and 4.5 L. For each magnitude of distension, intake was estimated on 3 consecutive days applying the procedures described above: without a balloon (d 1), with a balloon without distension (d 2), and with a balloon with distension (d 3). The sequence in which different magnitudes of distension were applied was 2.5, 1.8, and 4.5 L (Table 1). A manometer was used to measure air pressure inside the balloons and they were 13.8 (1.8 L) and 17.2 kPa (2.5 and 4.5 L).

Adaptation to Novel Feeds

Before conditioning, all animals (fistulated and nonfistulated) were offered beet pulp and wheat bran (particle size of 1 to 2 mm) from 0900 to 1000 h on 2 consecutive days to encourage lambs to eat or at least sample the novel feeds during the ensuing preference tests and conditioning protocols. From 1330 to 1730 h, all lambs received 1,600 g of ground alfalfa hay; at 1730 h, refusals were collected and no other feed was offered until the next day. Fistulated lambs consumed 118 ± 19 g of beet pulp, 153 ± 23 g of wheat bran, and 1,444 ± 65 g of alfalfa. Nonfistulated lambs consumed 87 ± 23 g of beet pulp, 112 ± 22 g of wheat bran, and 1,505 ± 89 g of alfalfa.

Preference Tests Before Conditioning

The purpose of 2- and 3-choice preference tests was to obtain a baseline preference before animals were conditioned with or without rumen distension and to balance groups based on individual lamb biases for wheat bran and beet pulp. Two-way choices were used to assign lambs within each category (fistulated, nonfistulated) to 2 groups (groups 1 and 2; n = 3). Lambs were stratified according to initial preference for 1 feed (e.g., wheat bran) and pairs of lambs were randomly assigned
to the 2 groups. Thus, differences between groups due to initial feed preferences were balanced.

**Two-Way Choice**

After the last day of adaptation to the novel feeds, lambs received wheat bran and beet pulp simultaneously for 15 min at 0900 h, and intake of each feed was determined. Percentage preference for each feed was calculated as \((\text{intake of a feed/total feed intake}) \times 100\).

From 1330 to 1730 h, all lambs were offered 1,600 g of alfalfa hay. No other feed was offered until the next day.

**Three-Way Choice**

The protocol was as described before, except that the day after the 2-way choice, lambs received a 3-way choice of wheat bran, beet pulp, and alfalfa hay (Table 1).

**Conditioning**

We hypothesized that rumen distension is aversive, and that relief from distension increases preference. Thus, the objective of conditioning was to allow animals to eat a novel feed (beet pulp, wheat bran) with rumen distension and to associate a different novel feed with relief from distension.

**Conditioning with Distension**

Before feeding, balloons were directed through the rumen cannulas of the fistulated lambs. Lambs in group 1 were then offered wheat bran and lambs in group 2 were offered beet pulp from 0900 to 0915 h. Refusals were collected and weighed and feed intake was determined. Immediately after weighing the refusals, all balloons were inflated with air to 2.5 L (d 1) and 4.5 L (d 2 to 5) for 30 min. With a balloon expanded in the rumen to 4.5 L, lambs evidenced distension of their left side and showed signs of discomfort (they walked in circles, lifted their back legs, stomped their feet, and lay down on their right side). At 0945 h lambs were fed again and conditioned to associate specific feeds with rumen contraction (recovery) by switching feeds; lambs in group 1 then were offered beet pulp, whereas lambs in group 2 were offered wheat bran. Within 2 min of offering lambs the novel feeds, the balloons were deflated (Table 1). Refusals were collected and weighed at 1000 h. After collecting refusals, balloons were removed from the rumen. From 1000 to 1330 h, lambs were without feed; they were fed alfalfa hay from 1330 to 1730 h. Refusals were collected and no other feed was offered.

### Table 1. Feeding protocol used to determine whether distension of the rumen depresses feed intake (distension of the rumen) and if distension and contraction of the rumen influences feed preference (conditioning and preference tests)

<table>
<thead>
<tr>
<th>Procedure and feed</th>
<th>Treatment</th>
<th>Time</th>
<th>Distension</th>
<th>Day</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distension of the rumen</td>
<td>Alfalfa Without a balloon</td>
<td>0900–1000 h</td>
<td>—</td>
<td>1, 4, 7</td>
</tr>
<tr>
<td>Alfalfa With a balloon without distension</td>
<td>0900–1000 h</td>
<td>2.5 L</td>
<td>3</td>
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<tr>
<td>Alfalfa With a balloon with distension</td>
<td>0900–0930 h</td>
<td>1.8 L</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Preference test before conditioning</td>
<td>Wheat bran Two-way choice. Simultaneous offer of wheat bran and beet pulp</td>
<td>0900–0915 h</td>
<td>—</td>
<td>10</td>
</tr>
<tr>
<td>Beet pulp</td>
<td>0900–0915 h</td>
<td>2.5 L</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Alfalfa</td>
<td>0900–0915 h</td>
<td>4.5 L</td>
<td>13–16</td>
<td></td>
</tr>
<tr>
<td>Conditioning with distension</td>
<td>Wheat bran Fed to group 1</td>
<td>0900–0915 h</td>
<td>—</td>
<td>11</td>
</tr>
<tr>
<td>Beet pulp</td>
<td>0900–0915 h</td>
<td>2.5 L</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Conditioning without distension (control)</td>
<td>Alfalfa Fed to group 2</td>
<td>0900–0915 h</td>
<td>—</td>
<td>13–16</td>
</tr>
<tr>
<td>Preference test after conditioning without distension (control)</td>
<td>Without a balloon</td>
<td>0900–1000 h</td>
<td>—</td>
<td>17–21</td>
</tr>
<tr>
<td>With a balloon with distension</td>
<td>0900–1000 h</td>
<td>2.5 L</td>
<td>22–23</td>
<td></td>
</tr>
<tr>
<td>Feed associated with recovery and basal diet</td>
<td>2.5 L</td>
<td>24–25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feed associated with recovery and basal diet</td>
<td>0900–0915 h</td>
<td>2.5 L</td>
<td>26</td>
<td></td>
</tr>
<tr>
<td>Preference tests for lambs conditioned without distension (control)</td>
<td>0900–0915 h</td>
<td>2.5 L</td>
<td>27</td>
<td></td>
</tr>
<tr>
<td>Preference tests for lambs conditioned without distension (control)</td>
<td>0900–0915 h</td>
<td>2.5 L</td>
<td>28–33</td>
<td></td>
</tr>
</tbody>
</table>

1Procedures were carried out in nonfistulated lambs as described for conditioning with distension, except that no balloon was introduced into the rumen of the animals.

2Two- and three-way preference tests as described during preference tests before conditioning.

3Two-way choice between beet pulp (treatment 1) or wheat bran (treatment 2) and alfalfa.

4Preference tests after conditioning were conducted in nonfistulated lambs (control) and thus no balloon was introduced into the rumen of the animals.
until the next day. Conditioning was conducted over 5 consecutive days.

**Conditioning Without Distension (Control)**

Nonfistulated lambs were conditioned as described in the previous section, except no balloon was introduced into the rumen so they did not experience the states of rumen distension or contraction (Table 1).

**Preference Tests After Conditioning**

**Without a Balloon.** We determined feed preferences by lambs after conditioning without distension. The lambs were offered 2- and 3-way choices on 2 consecutive days, as described during preference tests before conditioning, without a balloon in the rumen (Table 1).

**With a Balloon With Distension.** The day after tests without a balloon, we determined feed preferences by lambs experiencing ruminal distension. At 0900 h and before feeding, a rubber balloon attached to a rubber tube was directed through the rumen cannula of each lamb. Balloons were inflated to 2.5 L and then all animals were offered 2- and 3-way choices on 2 consecutive days as described previously (Table 1).

**Feed Associated with Recovery and Basal Diet.** The day after tests with a balloon with distension, lambs had a simultaneous offer of the feed associated with rumen contraction (recovery) during conditioning (group 1: beet pulp; group 2: wheat bran) and ground alfalfa hay (basal diet) in a 2-way choice, as described during preference tests before conditioning. Preference tests were conducted on 2 consecutive days, without (d 1) a balloon and with (d 2) a balloon with distension (2.5 L; Table 1).

**Preference Tests for Lambs Conditioned Without Distension (Control).** Preference tests were conducted as described in the previous sections, but no balloon was introduced into the rumen. Thus, the testing periods “without a balloon” and “with a balloon with distension” described previously were referred to as “without a balloon – test 1” and “without a balloon – test 2” for lambs conditioned without distension (Table 1).

**Statistical Analyses**

**Distension of the Rumen.** Feed intake for each feeding period (0 to 30 min, 30 to 60 min, and from 1000 to 1700 h) was analyzed as a factorial design with magnitude of distension (1.8, 2.5, and 4.5 L) and condition of the balloon (without a balloon, with a balloon without distension, and with a balloon with distension) as the main factors and lamb crossed with the main factors. A linear regression analysis was used to estimate the relationship between feed intake and log10[feed intake] and ruminal distension.

**Conditioning and Preference Tests.** Feed intake and preference were analyzed as a split-plot design with lambs nested within group (groups 1 and 2). Group (n = 2) was the between-subject factor, and feed (beet pulp, wheat bran) and treatment received during conditioning [distension, contraction (recovery)] were the within-subject factors in the split-plot. Day (conditioning; 1 to 5) or testing period (1 = preference tests before conditioning; 2 = preference tests without a balloon; or 3 = preference tests with a balloon with distension) were the repeated measures.

Analyses were computed using a mixed model (PROC MIXED; SAS Inst. Inc., Cary, NC). The model diagnostics included testing for a normal distribution of the error residuals and homogeneity of variance. Assumptions of normality and homogeneity of variance were met. Means were analyzed using pairwise differences (DIFF) of least squares means (LSMEANS).

**RESULTS**

**Distension of the Rumen.**

No differences in alfalfa intake were observed for any feeding period when lambs were tested without a balloon or with a balloon without distension in the rumen (P = 0.45 to 0.93; Figure 1). However, rumen distension (0 to 30 min) at the 3 magnitudes assessed (1.8, 2.5, and 4.5 L) reduced feed intake relative to conditions when there was no balloon in the rumen or when the balloon was in the rumen but not distended (P < 0.001; Figure 1).

Rumen distension continued to influence intake after balloons were deflated in ensuing feeding periods, but the effect was reversed. Lambs that had experienced rumen distension (0 to 30 min) showed a compensatory increase in feed intake when the balloons were deflated (30 to 60 min) relative to conditions when there was no balloon in the rumen or when the balloon was in the rumen but not distended (P = 0.006; Figure 1). Despite this compensation, average cumulative intake for the 0 to 60 min time interval was still decreased when lambs experienced (392 g) than when they did not experience ruminal distension (without a balloon: 592 g; with a balloon without distension: 588 g; P = 0.006; SEM = 48 g). Compensatory feed intake continued for the time interval 1000 to 1700 h. Averaged across the 3 levels of distension, lambs consumed 1,124 g of alfalfa from 1000 to 1700 h, whereas they ingested less when the balloons were not distended (928 g), or when they were not present in the rumen (970 g; P = 0.003; SEM = 40 g). This compensation resulted in similar total daily intakes for lambs experiencing or not experiencing rumen distension (P = 0.63).

Reductions in feed intake were proportional to the extent of distension, as shown by the linear decrease in feed intake with increasing ruminal distension (0 to 30 min; P < 0.001; R2 = 0.7). In contrast, intake increased
with level of distension when distension ceased during the ensuing feeding period of 30 min (30 to 60 min; \( P = 0.04; R^2 = 0.20 \); Figure 2). Similar trends were observed when intake values were log_{10}-transformed (0 to 30 min; \( P < 0.001; R^2 = 0.70 \); 30 to 60 min.; \( P = 0.04; R^2 = 0.20 \)).

**Conditioning**

**Conditioning With Distension.** Groups of lambs that experienced rumen distension after being offered either wheat bran (group 1) or beet pulp (group 2) reduced their intake across the 5 d of conditioning (day effect; \( P < 0.001 \)) in a similar fashion (group effect; \( P = 0.32 \); Figure 3). When feeds were switched and balloons were deflated, feed intake did not differ between groups (group effect; \( P = 0.74 \)) or across days (day effect; \( P = 0.24 \); Figure 3).

After conditioning with the test feeds, intake of the basal diet (alfalfa offered from 1330 to 1730 h) did not differ between groups (\( P = 0.93; 1,261 \) vs. 1,242 g; SEM = 155 g), but intake increased across days (day effect; \( P = 0.004 \)), likely in response to the daily decline in consumption of the tests feeds.

**Conditioning Without Distension (Control).** In contrast to conditioning with distension, groups of lambs that did not experience rumen distension after being offered either wheat bran (group 1) or beet pulp (group 2) increased their intake across time (day effect; \( P = 0.10 \); Figure 3). No difference between groups was observed (group effect; \( P = 0.68 \)).

When feeds were switched, intake of beet pulp (group 1) was greater and more variable than intake of wheat bran (group 2), which caused group (\( P = 0.09 \)) and day (\( P = 0.01 \)) effects and a group × day interaction (\( P = 0.01 \)).

After conditioning with the test feeds, intake of the basal diet did not differ between groups (1,433 vs. 1,408 g; SEM = 105 g; \( P = 0.88 \)), and intake did not change across days, except that intake decreased during d 3 (1,291 g) relative to the other days (average 1,453 g; SEM = 79 g; \( P = 0.004 \)).

**Preference Test Before Conditioning**

Lambs did not differ in initial preference for the test feeds to be associated with distension or contraction (recovery) (groups conditioned with distension) or for test feeds presented from 0900 to 0915 h or from 0945 to 1000 h (groups conditioned without distension) (\( P > 0.10 \); Figure 4).

**Preference Tests After Conditioning with Rumen Distension**

Two-Way Tests. Preference changed after conditioning: lambs strongly avoided feeds associated with rumen distension, and they preferred feeds associated with recovery (\( P = 0.001 \)). This pattern did not change when animals were tested without a balloon or with a distended balloon in the rumen (\( P = 0.32 \); Figure 4).

Averaged across preference tests, groups did not differ in their feed intake (group effect; \( P = 0.60 \)), and wheat bran and beet pulp were consumed in similar amounts during testing (130 and 134 g, respectively, SEM = 17; \( P = 0.86 \)), but intake of the test feeds was influenced by distension/contraction experienced during conditioning. Intake was decreased regardless of the type of feed (wheat bran or beet pulp) when feeds were conditioned with distension (wheat bran 1 and 24 g; beet pulp 10 and 41 g) compared with when feeds were conditioned with rumen contraction (recovery) (wheat bran: 211 and 235 g; beet pulp: 192 and 284 g), for
periods of testing with a distended balloon or without a balloon, respectively (SEM = 30; group × feed × period interaction; *P* < 0.001).

Intake of feeds conditioned with distension decreased from before conditioning (151 g) to the testing periods after conditioning: without a balloon (32 g) and with a balloon with distension (6 g; *P* < 0.001; SEM = 21). In contrast, intake of feeds associated with rumen contraction (recovery) increased from before conditioning (141 g) to testing after conditioning: without a balloon (259 g) and with a distended balloon (202 g; *P* < 0.001; SEM = 21).

**Three-Way Tests.** As in 2-way preference tests, preference in 3-way tests changed after conditioning. Lambs strongly avoided feeds associated with rumen distension and they showed a robust preference for the feeds associated with rumen contraction (recovery) (treatment × period interaction; *P* < 0.001; Figure 4). This pattern did not change when animals were tested without a balloon or with an inflated balloon inside the rumen (*P* > 0.33; Figure 4).

Averaged across preference tests, groups did not differ in their feed intake (group effect; *P* = 0.86), and feeds were consumed in similar amounts during testing.
(feed effect; $P = 0.26$), but intake of the test feeds was affected by distension/contraction experienced during conditioning. Intake was decreased regardless of the type of feed (wheat bran or beet pulp) when feeds were conditioned with distension (wheat bran 0 and 25 g; beet pulp 2 and 24 g) than when feeds were conditioned with rumen contraction (recovery) (wheat bran 230 and 176; beet pulp 289 and 131 g; for periods of testing with and without an inflated balloon in the rumen, respectively; SEM = 34; group × feed × period interaction; $P < 0.001$).

Intake of alfalfa and preference for alfalfa did not change during preference tests (Figure 4), except that alfalfa intake was decreased when animals were tested with a distended balloon (40 g) than when they were tested before conditioning (90 g; $P = 0.06$; SEM = 25). However, intake of the feeds associated with rumen contraction (recovery) did not decline during testing with a distended balloon (154 g) relative to before conditioning (133 g; $P = 0.31$), and intake was greater during testing without a balloon (259; $P < 0.001$).

**Feed Associated with Recovery and Basal Diet.** Averaged across test periods, lambs preferred the feeds conditioned with recovery (rumen contraction) to the basal diet (191 vs. 86 g; SEM = 37; $P = 0.10$). This pattern did not change across testing periods ($P = 0.37$; Figure 4).

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**Conditioning with distension**

**Conditioning without distension**

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**Figure 3.** Intake of wheat bran and beet pulp by lambs conditioned with contrasting extents of rumen distension. When conditioning with distension, lambs received either wheat bran (group 1) or beet pulp (group 2) from 0900 to 0915 h, and balloons were then inflated within the rumen of all animals. From 0945 to 1000 h lambs were offered either beet pulp (group 1) or wheat bran (group 2) and the balloons were deflated (recovery). When conditioning without distension, lambs received the same feeding protocol but balloons were not present. Values are means for 3 animals per group; vertical bars are SE.
**Preference Tests After Conditioning Without Rumen Distension (Control)**

**Two-Way Tests.** Lambs that did not experience rumen distension did not modify their pattern of preference after conditioning relative to tests conducted before conditioning \( (P = 0.87; \text{Figure 4}) \). Averaged across preference tests, groups did not differ in their feed intake \( (\text{group effect; } P = 0.24) \), and wheat bran and beet pulp were consumed in similar amounts during testing \( (138 \text{ and } 165 \text{ g, respectively, } \text{SEM} = 16; P = 0.30) \). Intake of the test feeds across testing periods was not influenced by the treatment \( (\text{order of feed presentation}) \) applied during conditioning \( (\text{treatment} \times \text{period interaction; } P = 0.73) \).

Intake of wheat bran did not change across all the testing periods \( (P > 0.10) \), whereas intake of beet pulp increased across testing periods from 115 g before conditioning to 215 g during test 2 after conditioning \( (\text{SEM} = 22; P < 0.05) \).
Three-Way Tests. As in 2-way preference tests, preference in 3-way tests did not change from before to after conditioning (treatment × period interaction; \( P = 0.67 \); Figure 4).

Averaged across preference tests, groups did not differ in their feed intake (group effect; \( P = 0.35 \)), but lambs ingested more alfalfa (127 g) and beet pulp (164 g) than wheat bran (58 g) (feed effect; SEM = 14; \( P = 0.003 \)). Intake of test feeds during preference tests was not affected by the treatment (order of feed presentation) experienced during conditioning (treatment × period interaction; \( P = 0.38 \)). Averaged across preference tests, lambs ingested 102 and 120 g of the feeds offered from 0900 to 0915 h and from 0945 to 1000 h during conditioning, respectively, and 127 g of alfalfa (SEM = 0.67; Figure 4).

Feed Associated with Recovery and Basal Diet. No differences were observed in feed preference. Lambs ingested similar amounts of the feeds during conditioning (0945 to 1000 h) and alfalfa (207 and 135 g; SEM = 30; \( P = 0.17 \)). This pattern did not change across testing periods (\( P = 0.37 \); Figure 4).

DISCUSSION

Distension of the Rumen

Inflating an air-filled balloon in the rumen decreased feed intake in proportion to the extent of distension. Inflating rubber balloons with water also results in dose-dependent depressions in feed intake (Campling and Balch, 1961; Anil et al., 1993), but water likely distends primarily the ventral walls of the rumen. To our knowledge, ours is the first study to use air to fill the balloons. This effect likely affects the dorsal sac of the rumen (J. L. Miner, University of Nebraska, Lincoln; personal communication) and is more likely to mimic distension due to gas accumulation in the rumen during bloat (Cheng et al., 1998). Gas accumulation can increase intraruminal pressures to values >9.34 kPa (Lippke et al., 1972). During our study, air pressure inside the balloons was from 13.8 to 17.2 kPa. Distending the rumen with balloons inflated with gas to 1.8 and 2.5 L created reductions in feed intake compared with those observed when balloons were inflated with water in the rumen of sheep (1.6 to 2.4 L; Miner et al., 1990). Greater magnitudes of distension seemed to induce a smaller effect on intake reduction than did lesser magnitudes of distension. Beyond a certain threshold (2.5 L in our study) the anorectic effects of distension were likely dampened due to overstimulation or habituation of tension receptors in the rumen.

When balloons were deflated (30 to 60 min), compensatory feed intake was observed in lambs that previously experienced rumen distension. The rapid compensation in feed intake from 30 to 60 min after distension suggests that animals recovered quickly from the previous state of distension, but they were not able to compensate completely during the first hour after deflation, and intake was decreased when lambs experienced rumen distension than when they did not, as in previous studies (Grovum, 1979). Lambs were able to fully compensate during the time interval from 1000 to 1700 h, and total daily intakes did not differ when animals were tested with or without distension.

No differences in feed intake were observed when lambs were tested without a balloon or with a balloon without distension in the rumen, which suggests that the balloon per se did not influence feeding. Rather, distension and contraction of the balloon were the cues that animals used to modify their feeding behavior. Thus, when we conditioned sheep without intraruminal distension (controls), we did not use balloons.

Conditioning

During conditioning lambs were offered either wheat bran or beet pulp for 15 min followed by ruminal distension. Even when animals ingested the test feeds before experiencing distension, they still reduced feed intake as conditioning progressed, which suggests that the negative postingestive effects of distension caused the reduced feed intake. Similar reductions in feed intake occur when animals acquire feed aversions after ingesting gastrointestinal toxins (e.g., LiCl, tannins; Burritt and Provenza, 1989; Provenza et al., 1990). In contrast, lambs that experienced the same feeds and for the same sequences and time intervals, but without distension (controls; lambs conditioned without distension), did not reduce intake of test feeds during conditioning.

Preference Tests

Lambs strongly avoided the feed—wheat bran or beet pulp—ingested before experiencing rumen distension in 2- and 3-way preference tests. Thus, rumen distension evidently caused a feed aversion, which appeared similar to those induced by gastrointestinal toxins (Provenza, 1995, 1996; Provenza and Villalba, 2006). Thus, mechanoreceptors in the rumen, in addition to signaling satiety, may also stimulate the emetic system of the midbrain and brain stem and cause feed aversions (Mitchelson, 1992; Provenza, 1996). The satiety hypothesis predicts that eating any feed to satiety is likely to cause a mild aversion because of feedback from chemo-, osmo-, and mechanoreceptors throughout the gastrointestinal tract (Provenza, 1996). Animals are likely to become averse even to nutritious feeds because satiety (satisfied to the full) and surfeit (filled to nauseating excess) represent a continuum and there is a fine line between satiety and aversion. Thus, transient aversions as a consequence of distension of the rumen may be one of the mechanisms involved in the normal control of feed intake (see Bárdos, 2001).

As during feed aversion learning with gastrointestinal toxins (Burritt and Provenza, 1991), lambs in our study learned to avoid the feed consumed shortly before experiencing malaise. In contrast, inflating a water balloon...
before rather than after a meal of concentrates did not condition an aversion in cows (Klaiss and Forbes, 1999). Temporal relationships between a stimulus (flavor of a feed) and its consequence (distension) are crucial for learning, and feed ingestion must precede the gastrointestinal consequences of feed ingestion. Short delays between feed consumption and the onset of distension produce strong and rapid conditioning (Mazur, 1994).

Lambs markedly increased their preference for feeds associated with relief from rumen distension. Immediately after lambs were offered the specific test feeds (stimulus), the distended balloons inside their rumens were deflated (consequence), and relief from distension likely increased preference for those feeds. Animals are more likely to learn about the benefits of a feed (medicine) that alleviates a negative internal state when they experience illness and then ingest the medicine that leads to recovery (Villalba and Provenza, 2001, 2002). Sheep learn to ingest 3 different medicines to relieve 3 different states of malaise when relief from illness quickly follows medicine ingestion. In contrast, control lambs that ate the same feeds and medicines but disassociated temporally (so they did not recuperate from illness) never learned to use the medicines (Villalba et al., 2006).

We predicted that if lambs associated specific feeds with recovery (contraction), their preference for those feeds would increase when they were experiencing rumen distension (when need for the feed associated with relief was greater) relative to periods when they did not. However, preferences for feeds associated with recovery were already very high when testing occurred without a balloon and did not change when animals were tested with a distended balloon in the rumen. Nevertheless, there are 3 lines of evidence suggesting that lambs increased preference for the feeds associated with rumen contraction, and that they did not simply avoid feeds associated with rumen distension. First, preference for alfalfa (a feed not experienced during conditioning) or for feeds ingested by lambs conditioned without distension (controls) did not change across preference tests, whereas preference for feeds associated with rumen contraction increased after conditioning. Second, intake of alfalfa and of feeds associated with distension decreased during tests with a distended balloon relative to tests without a balloon, likely because of the satiating effects of distension, whereas intake of the feeds associated with recovery did not decline when tested with a distended balloon. Finally, lambs conditioned with rumen distension preferred the feed associated with recovery to the basal diet during preference tests between those 2 feeds. In contrast, lambs conditioned without distension (control) did not show such preference.

Pasture bloat usually occurs when animals graze wheat pasture or lush legumes such as alfalfa and clover. The capture of ruminal gases in a polysaccharide slime layer increases intraruminal pressure, which suppresses nerve receptors that regulate eructation (Cole and Boda, 1960). Animals often develop strong preferences for feeds that cause bloat, evidently because of the positive effects of nutrients conditioning preferences and the lack of novelty of the feeds. If animals experience the positive effects of nutrients over an extended time, and only occasionally experience the aversive effects of bloat, they are likely to acquire a strong preference, not an aversion. Animals acquire the strongest aversions when aversive consequences immediately follow ingestion of a novel feed.

Concluding Remarks

Our study shows that lambs learn about the negative effects of ruminal distension and suggests that they learn to prefer feeds associated with relief from distension. Thus, it may be possible to train animals to regulate consumption of bloat-inducing pastures by also giving them access to plants that alleviate bloat. Current recommendations to prevent bloat include restricting the availability of lush legumes in pastures and preloading animals on dry roughage or grass to reduce consumption of bloat-inducing pastures. Alternatively, condensed tannins in plants such as birdsfoot trefoil and sanfoin have the potential to reduce the incidence of bloat as they reduce microbial activities, polysaccharide slime, and ruminal gas production (Min et al., 2005, 2006). Further research is required to determine whether livestock learn to prefer tannin-containing plants and supplements that reduce the incidence of bloat when foraging in pastures containing bloat-inducing species.

LITERATURE CITED


