Effect of selenium concentration on feed preferences by cattle and sheep

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ABSTRACT: Selenium-accumulator plants are reputed to be unpalatable to livestock. The objective of this study was to determine if sheep and cattle could discriminate between forages and feeds with different concentrations of Se. In the first study, cattle and sheep preferences for intermediate wheatgrass (Thinopyrum intermedium), alfalfa (Medicago sativa), and western aster (Symphyotrichum ascendens) of varying Se concentrations were assessed. The Se concentrations ranged from 0.8 to 50 mg/kg (DM) in grass, 1.4 to 275 mg/kg in alfalfa, and 4 to 4,455 mg/kg in aster. Selenium concentration had no influence (P > 0.05) on the initial or subsequent preferences of sheep or cattle for grass or alfalfa. Cattle developed an aversion to aster after consuming 95% of the plant material during the first brief exposure and subsequently refused to eat any aster. Sheep consumption of aster was variable, but their preference was not driven by Se concentration. In the next study, cattle and sheep were offered pellets at 1.5% of BW (as fed) that contained increasing concentrations of Se from aster (control and 5, 25, 45, and 110 mg/kg Se). In trial 1, all pellets were offered. In Trials 2 and 3, all pellets were offered with the exception of the 5 mg/kg Se pellet and the 5 and 25 mg/kg Se pellets, respectively. In trial 1, consumption of the control pellet by cattle was greater on all days compared with other Se pellets (P < 0.001). Cattle ate more (P < 0.001) of the 5 mg/kg Se pellet than the higher Se pellets on d 3, 4, and 5. Sheep ate greater amounts of the control and 5 and 110 mg/kg Se pellets compared with the 25 and 45 mg/kg Se pellets (P < 0.0001) on d 1, and sheep consumed primarily the control and 5 mg/kg Se pellets thereafter. In trial 2, cattle and sheep consumed more (P < 0.0001) of the control Se pellet than the 25, 45, and 110 mg/kg Se pellets. In trial 3, cattle consumption of the control and 45 and 110 mg/kg Se pellets differed on d 2 and 3 (P < 0.001), except there was no difference (P > 0.95) in cattle consumption of the control and 45 mg/kg Se pellets on d 1. Sheep consumed primarily the control and 45 mg/kg Se pellets. We conclude that high Se concentrations in fresh forages had no effect on initial consumption by cattle or sheep. When given Se pellets, initial responses were variable, but the results indicate that cattle and sheep adjusted their intake over time to avoid excessive intake of Se.

Key words: cattle, intake, preference, selenium, sheep, toxicity

INTRODUCTION

Selenium is an element required for the activity of many enzymes and other proteins, which support several physiologically important roles in animal immunity, reproduction, and production (Underwood and Suttle, 1999). Selenium has the least dietary essential to toxic ratio of any element required by mammals (Koller and Exon, 1986). Forage Se concentrations >5 mg/kg are presumed to be toxic to grazing ruminants (NRC, 2000; Raisbeck, 2000).

Selenium-accumulator plants are reputed to be unpalatable to grazing livestock, particularly at high Se concentrations (Beath, 1920, 1921; Beath et al., 1935). Anecdotal accounts suggest that livestock consume Se-accumulator plants only when other forage is scarce (Beath, 1920; Raisbeck et al., 1998; Davis et al., 2000). The avoidance or poor palatability of accumulator plants is often attributed to the flavor or odor of Se (Burrows and Tyrl, 2001). Conditioned-food aversions

1The authors thank Kermit Price and Katie Lott for excellent technical assistance, Rex Probst for assistance with the animals, Susan Durham for help with the statistical analysis, and Harold Winger and Mary Hubbard of the Utah State Veterinary Diagnostic Laboratory for Se analysis.

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Received April 15, 2013.
Accepted September 12, 2013.
may also play a role in deterring livestock consumption of seleniferous plants (Pfister et al., 2010). Even so, grazing animals periodically ingest chronically intoxicating or acutely toxic concentrations of seleniferous plants when other forages are abundant (Tiwary et al., 2006; Davis et al., 2012).

Limited information is available about the effect of Se concentration in feeds or forages on preference or palatability to livestock. The objective of this study was to determine if sheep and cattle could discriminate between forages and feeds with different concentrations of Se. In the first study, freshly harvested forages with differing Se concentrations were offered to cattle and sheep. In the second study, cattle and sheep were fed alfalfa pellets containing various concentrations of Se.

**MATERIALS AND METHODS**

All animal procedures were approved by the Utah State University Institutional Animal Care and Use committee and were performed under veterinary supervision.

**Selenium Preference Trials with Fresh Wheatgrass, Aster, and Alfalfa**

Eight Hereford × Angus steers (411 ± 13 kg; 2 yr old) and 8 crossbred wethers (76 ± 3 kg; 1 yr old) were used. All animals were fed alfalfa hay containing <0.3 mg/kg Se for 2 mo before the study. All animals were initially made tractable by daily handling and hand feeding for 1 mo. To implement the preference procedure, individual animals were trained to enter a 5- by 5-m pen (cattle) or a 2- by 2-m pen (sheep), with food boxes evenly spaced along each wall. Training consisted of placing a small amount of concentrate feed in each box; animals quickly learned to investigate each box after an overnight fast. Animals were trained daily for 2 wk to enter the pen and to quickly investigate and eat from all the boxes during a 5-min period.

The same procedure was used for all fresh forages tested in this study. Sheep and cattle were offered 5 different intermediate wheatgrass [Thinopyrum intermediate (Host) Barkworth & D.R. Dewey], 4 different western aster [Symphyotrichum ascendens (Lindl.) G.L. Nesom], and 3 different alfalfa (Medicago sativa L.) collections (Table 1). Within each forage collection a concerted effort was made to find a control (i.e., Se concentration <0.3 mg/kg) and other collections differing substantially in Se concentration (Table 1). Two days before the trials began with the each type of plant, forages in various locations growing on or near reclaimed phosphate mine sites in southeastern Idaho (near Soda Springs, ID, approximately 150 km from Logan, UT), many with a history of high Se concentrations (Davis et al., 2012), were sampled and the Se concentrations determined by inductively coupled plasma–mass spectrometry (ICP–MS). Based on these data, locations were selected to include forages with a wide range of Se concentrations. Voucher specimens of plants from each location were deposited in the USDA Poisonous Plant Research Laboratory herbarium.

During the trials a bulk collection of each forage was freshly harvested each morning at 0800 to 0900 h, transported to Logan, UT, clipped into 3-cm lengths, thoroughly mixed, and offered simultaneously in the testing pen at about 1100 to 1300 h to each individual animal. Subsamples were collected and frozen each day from the

### Table 1. Selenium and nutrient content (DM basis) of forages used in preference trials with cattle and sheep. All forages were freshly harvested daily during July 2012 and offered to cattle and sheep in pen trials

<table>
<thead>
<tr>
<th>Trial</th>
<th>Forage1</th>
<th>Elevation, m</th>
<th>Se concentration,2 mg/kg ± SE</th>
<th>CP,3 %</th>
<th>NDF, g/100 g</th>
<th>IVTD,3 g/100 g</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fresh grass</td>
<td>Grass no. 1</td>
<td>1,930</td>
<td>0.77 ± 0.09</td>
<td>9.9</td>
<td>66.4</td>
<td>72.0</td>
</tr>
<tr>
<td>Fresh grass</td>
<td>Grass no. 2</td>
<td>2,042</td>
<td>17.8 ± 0.2</td>
<td>11.4</td>
<td>64.1</td>
<td>76.4</td>
</tr>
<tr>
<td>Fresh grass</td>
<td>Grass no. 3</td>
<td>2,000</td>
<td>29.1 ± 3.8</td>
<td>9.6</td>
<td>62.8</td>
<td>77.1</td>
</tr>
<tr>
<td>Fresh grass</td>
<td>Grass no. 4</td>
<td>1,987</td>
<td>50.4 ± 5.0</td>
<td>8.8</td>
<td>64.8</td>
<td>74.7</td>
</tr>
<tr>
<td>Fresh grass</td>
<td>Grass no. 5</td>
<td>1,996</td>
<td>100.2 ± 4.4</td>
<td>9.1</td>
<td>65.1</td>
<td>69.0</td>
</tr>
<tr>
<td>Fresh alfalfa</td>
<td>Alfalfa no. 1</td>
<td>1,550</td>
<td>1.4 ± 0.7</td>
<td>23.1</td>
<td>36.9</td>
<td>78.1</td>
</tr>
<tr>
<td>Fresh alfalfa</td>
<td>Alfalfa no. 2</td>
<td>1,987</td>
<td>107.3 ± 30</td>
<td>18.5</td>
<td>45.6</td>
<td>70.5</td>
</tr>
<tr>
<td>Fresh alfalfa</td>
<td>Alfalfa no. 3</td>
<td>1,981</td>
<td>275 ± 36</td>
<td>19.9</td>
<td>45.9</td>
<td>69.8</td>
</tr>
<tr>
<td>Fresh aster</td>
<td>Aster no. 1</td>
<td>1,972</td>
<td>3.97 ± 1.3</td>
<td>17.2</td>
<td>42.0</td>
<td>76.9</td>
</tr>
<tr>
<td>Fresh aster</td>
<td>Aster no. 2</td>
<td>1,991</td>
<td>1,270 ± 62</td>
<td>13.9</td>
<td>42.9</td>
<td>75.5</td>
</tr>
<tr>
<td>Fresh aster</td>
<td>Aster no. 3</td>
<td>1,994</td>
<td>1,716 ± 245</td>
<td>10.2</td>
<td>40.9</td>
<td>75.5</td>
</tr>
<tr>
<td>Fresh aster</td>
<td>Aster no. 4</td>
<td>1,998</td>
<td>4,455 ± 560</td>
<td>12.8</td>
<td>42.3</td>
<td>74.1</td>
</tr>
</tbody>
</table>

1All the grasses were *Thinopyrum intermedium* (intermediate wheatgrass); all the alfalfa were *Medicago sativa*; all the asters were *Symphyotrichum ascendens* (western aster). The collection sites were on public or private lands on or near mine reclamation sites in southeastern Idaho, near Soda Springs.

2The Se concentration is in mg/kg and shown as the average ± SE over the days of the trial. The grass trial was 5 d, the alfalfa trial was 3 d, and the western aster trial was 4 d in duration. Forages at each site were prescreened and subsampled before the trials began to determine the range of Se concentrations, and forages were collected on each trial day, clipped into 3-cm lengths, thoroughly mixed, and offered to cattle and sheep by midday.

3Crude protein (%) = N × 6.25; IVTD = in vitro true digestibility. All analyses were performed on composited daily subsamples of the harvested forage.
forages offered for later analysis. With each fresh forage, the number of days the forage was offered was the same as the number of forage choices. The sheep were offered 50 g (as fed) of each harvested forage in each food box for 5 min whereas the steers were offered 200 g (as fed) of harvested material in each food box for 5 min. Each food box was equally spaced along the pen walls, and each forage was rotated to a new position each day to mitigate position bias; therefore, each feed occupied each position once during each trial. The experiment used the same number of forages, days, and positions within the pen (Borman et al., 1991; Pfister et al., 1996). There was a 4-d period between the grass and alfalfa preference trials and a 3-d period between the alfalfa and aster preference trials during which animals were fed alfalfa hay (<0.3 mg/kg Se) for ad libitum intake.

**Selenium Preference Trials with Pelleted Forage of Varying Selenium Concentrations**

Three trials using pellets with predetermined Se concentrations were conducted after the fresh forage trials. Alfalfa pellets were commercially made with the specific addition of calculated amounts of previously analyzed western aster to provide pellets with target Se concentrations of 5, 25, 45, and 110 mg/kg (Table 2). Western aster growing on seleniferous soils may contain >2,000 mg/kg Se (Davis et al., 2012). Alfalfa (control) pellets with no added western aster were made at the same time as the Se pellets using alfalfa containing <0.3 mg/kg Se.

Sheep \( (n = 4) \) and steers \( (n = 4) \) from the fresh forage trials were randomly selected for inclusion in these 3 trials. The animals were returned to normal Se status through feeding of alfalfa hay (<0.3 mg/kg Se) for 7 wk immediately before the 3 trials began. The Se status of each animal was determined by ICP–MS analysis of whole blood samples. Throughout the 3 trials, the animals were housed individually in 3- by 3-m pens in a covered barn with free access to Se-free salt blocks and water. They were adapted for 7 d to the pens and fed only the control pellets at 2.5% of BW (as fed) during the adaptation period. After the first 2 d, the cattle and sheep ate all the alfalfa pellets offered each day for the remainder of the adaptation period.

The 3 trials also used a design with positions, days, and pellets of various Se concentrations as factors (Borman et al., 1991). Each trial used the same number of days and positions as there were pellet choices. Each Se pellet was rotated to a new position within each pen each day of the trial. Each type of pellet was offered in each feed box at 1.5% of BW (as fed) for 8 h each day from 0800 to 1600 h. The intent was that animals could not reach satiety from eating just one choice. Refusals were weighed at the end of the feeding period (i.e., 1600 h), and no other feed was given. In trial 1, all pellets were offered. In Trials 2 and 3, all pellets were offered with the exception of the 5 mg/kg Se pellet and the 5 and 25 mg/kg Se pellets, respectively. There was a 3-d period between each trial.

**Preference Trial with Western Aster Containing Low Selenium Concentrations**

A similar trial as previously noted was conducted with four 1-yr-old crossbred ewes (70 ± 5 kg; naïve to western aster) to determine if the western aster used to make Se pellets in the previous trials influenced preference. Western aster growing in southeastern Idaho with low Se concentrations (<2 mg/kg) was harvested, air dried, ground to pass a 2-mm screen, mixed with ground alfalfa hay, and made into 0.4, 1.2, and 4.1% (as fed) aster pellets; a control pellet was made with only ground alfalfa hay. These 0.4, 1.2, and 4.1% aster pellets contained a ratio of aster to alfalfa that corresponded to 10, 30, and 110 mg/kg Se pellets, respectively. Sheep were trained as previously described in individual pens, and a 4-d trial was conducted to determine pellet intake with the 4 different pellets and 4 feeding locations within the pens over 4 d. The pellets were rotated through the positions in the pens each day. Each animal was offered each pellet at 1.7% of BW (as fed) daily; sheep were given 24 h access to the pellets.

**Table 2.** Target and actual concentration of Se (mg/kg) and the nutrient content of pellets used in pen trials to determine preference of steers and sheep for pellets differing in Se concentration

<table>
<thead>
<tr>
<th>Preference trial</th>
<th>Target Se concentration, (^1) mg/kg</th>
<th>Actual Se concentration, (^1) mg/kg</th>
<th>CP content, (^2) %</th>
<th>NDF, g/100 g</th>
<th>IVTD, g/100 g</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.3</td>
<td>0.13</td>
<td>18.9</td>
<td>43.1</td>
<td>71.9</td>
</tr>
<tr>
<td>1</td>
<td>5</td>
<td>6.07</td>
<td>19.9</td>
<td>40.5</td>
<td>76.2</td>
</tr>
<tr>
<td>1</td>
<td>25</td>
<td>22.4</td>
<td>20.8</td>
<td>42.6</td>
<td>75.4</td>
</tr>
<tr>
<td>1</td>
<td>45</td>
<td>47.7</td>
<td>19.6</td>
<td>41.3</td>
<td>74.9</td>
</tr>
<tr>
<td>1</td>
<td>110</td>
<td>105.5</td>
<td>18.7</td>
<td>42.8</td>
<td>70.6</td>
</tr>
<tr>
<td>2</td>
<td>0.3</td>
<td>0.28</td>
<td>18.4</td>
<td>40.4</td>
<td>76.0</td>
</tr>
<tr>
<td>2</td>
<td>25</td>
<td>28.8</td>
<td>20.5</td>
<td>41.1</td>
<td>75.8</td>
</tr>
<tr>
<td>2</td>
<td>45</td>
<td>41.0</td>
<td>19.4</td>
<td>42.2</td>
<td>72.9</td>
</tr>
<tr>
<td>2</td>
<td>110</td>
<td>111.3</td>
<td>20.1</td>
<td>40.6</td>
<td>73.2</td>
</tr>
<tr>
<td>3</td>
<td>0.3</td>
<td>0.13</td>
<td>19.1</td>
<td>42.1</td>
<td>73.8</td>
</tr>
<tr>
<td>3</td>
<td>45</td>
<td>47.0</td>
<td>19.3</td>
<td>41.9</td>
<td>72.8</td>
</tr>
<tr>
<td>3</td>
<td>110</td>
<td>121.7</td>
<td>19.6</td>
<td>42.0</td>
<td>71.6</td>
</tr>
</tbody>
</table>

\(^1\) Pellets were commercially made from alfalfa hay with the addition of *Symphyotrichum ascendens* (western aster) to reach the desired Se concentration (DM). The actual Se concentrations were determined from subsamples taken each day during the trial and then composited for analysis.

\(^2\) All values are on a DM basis. CP content (%) calculated as N × 6.25. Se, CP, NDF, and in vitro true digestibility (IVTD) analyses were done on subsamples of pellets collected daily during the trials.
Blood Collection

Whole blood samples were taken periodically (Table 3) to verify the Se status of the animals. Whole blood samples (5 mL) were collected via jugular venipuncture using sterile metal-free tubes (Tyco Healthcare Group LP, Mansfield, MA) with 10.5 mg EDTA (Na₂). Whole blood samples were stored at 4°C until analyzed.

Selenium Analysis of Forages and Whole Blood

Selenium in plant material and whole blood was analyzed using ICP–MS. Plant tissue was digested via a modification of U.S. Environmental Protection Agency method 3050 (Kingston and Walter, 1992). Digestions were performed in screw-cap Teflon tubes, using 0.5 g of ground plant material in 10 mL of trace metal grade nitric acid at 90°C for 2 h with the caps loose on the tubes. The plant digests were diluted in 5% nitric acid with 18.3 MΩ ultrapure water before analysis.

For whole blood analysis, samples were prepared as described by Tiwary et al. (2006). Briefly, a 750-μL aliquot of whole blood was introduced into a 10-mL Oak Ridge Teflon digestion tube (Nalge Nunc International, Rochester, NY). An equal amount (750 μL) of trace metal-grade nitric acid was added to the digestion tubes, and the caps were sealed. The tubes were heated on a heat block at 90°C for 2 h to digest the sample without unscrewing of the caps. After digestion, tubes were allowed to cool, and contents were transferred to another trace-metal-free tube. One milliliter of the digest (750 μL of sample plus 750 μL of nitric acid) was transferred into another trace-metal-free tube containing 9.0 mL of ultrapure water, to make a 5% nitric acid matrix. After vortexing, the samples were analyzed using ICP–MS.

Samples prepared as per the aforementioned digestion methods were analyzed with an ELAN 6000 ICP–MS (PerkinElmer, Shelton, CT). Quantification of Se was performed by the standard addition method, using a 4-point standard curve. A quality control sample (in similar matrix) was analyzed after every 5 samples, and the analysis was considered acceptable if the Se concentration of the quality control sample fell within ±5% of the standard reference value for the quality control.

Nitrogen Analysis of Feed

Subsamples of both forages and pellets were taken on a daily basis throughout the experimental periods, composited, ground to pass a 1-mm screen in a Wiley mill (Thomas Scientific, Swedesboro, NJ), and analyzed for DM, CP (N × 6.25; LECO FP-528 Nitrogen Analyzer; LECO Corp., St. Joseph, MI), NDF (ANKOM Fiber Analyzer system; ANKOM Technology, Macedon, NY), and in vitro true digestibility (IVTD; ANKOM Daisy II system; ANKOM Technology). The NDF procedure was modified by addition of heat-stable amylase (Sigma Chemical, St. Louis, MO). All analyses are reported on a DM basis.

Statistical Analysis

The fixed effects of position, day, treatment (i.e., different forages or pellets), and the day × treatment interaction on proportion consumed (% of offered) were assessed using a generalized linear mixed model with a β distribution, a logit link, and Laplace estimation. Pen (i.e., different animals) was a random effects blocking factor. Pairwise comparisons among treatment means within a given day were adjusted for familywise Type I error (α = 0.05) using the Tukey-Kramer method. The analysis was done using the GLIMMIX procedure in SAS/STAT 12.1 (SAS Inst. Inc., Cary, NC). For the analysis of Se intake (mg/kg BW) and for pellet intake (% of BW) in the phase II trials, means for each animal were used in an ANOVA (Proc ANOVA in SAS) to test for differences in days, and the Tukey procedure was used to compare day means after a significant (P < 0.05) F-test.

RESULTS

Selenium Concentration in Forage and Pellets

The Se concentrations of the fresh forages and custom-made pellets offered to cattle and sheep are given in Tables 1 and 2. The low Se aster pellets used in the sheep preference trial to determine if aster influenced pellet
intake contained <0.3 mg/kg Se. As expected the Se concentrations in the fresh forages varied greatly depending on the plant species and the collection location. The Se pellets were within an acceptable range of the target Se concentrations.

**Selenium Concentrations in Blood**

Sheep had whole blood Se concentrations of 0.14 ± 0.02 mg/kg (Table 3) when the study began, slightly below the normal range (0.15 to 0.50 mg/kg) according to Puls (1994). Cattle began the study with blood Se concentrations of 0.17 ± 0.017 mg/kg (Table 1). Normal whole blood Se concentrations for cattle are 0.20 to 1.20 mg/kg (Puls, 1994); however, in this region of the western United States, typical Se concentrations in whole blood of cattle as measured at the Utah State Veterinary Diagnostic Laboratory are between 0.15 and 0.30 mg/kg (J.O. Hall, Utah Veterinary Diagnostic Laboratory personal communication).

Additional blood samples were taken periodically after the cattle consumed high-Se western aster on d 1 of that portion of the fresh forage trial. Two days after eating the high-Se western aster, the Se concentration in whole blood of cattle increased to about 0.5 mg/kg (Fig. 1) with a gradual decline thereafter. During the course of the 3 preference trials, Se concentrations in sheep whole blood rose to >0.80 mg/kg at the end of the study (Table 3) whereas Se concentrations in cattle blood peaked at >0.7 mg/kg.

**Preference Trial with Western Aster Containing Low Selenium Concentrations**

The pellets in this trial were nutritionally similar (DM), with 23.3 to 24.9% CP, 30.8 to 32.4% NDF, and in vitro digestibility from 78.7 to 82.5%. Sheep did not discriminate against the aster contained in the pellets. There were treatment (i.e., pellet) and day effects ($P < 0.05$) for consumption but no treatment × day interaction ($P > 0.05$). Sheep ate an average of 59 ± 8, 30 ± 4, 44 ± 5, and 49 ± 6% of the control and 0.4, 1.2, and 4.1% aster pellets, respectively, over the 4-d trial. Consumption of control and 4.1% aster pellets differed ($P < 0.05$) from the 0.4% aster pellet, but consumption of the 0.4 and 1.2% pellets did not differ ($P > 0.10$).

**Selenium Preference Trials with Fresh Wheatgrass, Aster, and Alfalfa**

There was no evidence for initial selection or discrimination based on Se concentration among the 5 grass (Fig. 2), the 3 alfalfa (Fig. 3), or the 4 aster (Fig. 4) collections. For the grass and alfalfa trials, there were no day or treatment differences ($P > 0.10$) or treatment × day interactions ($P > 0.10$) for cattle or sheep. For both cattle and sheep, there were day effects for consumption of western aster ($P < 0.01$) but no treatment differences or treatment × day interactions ($P > 0.15$) among the various western aster collections. Cattle ate the fresh aster only on d 1 of the 4-d trial and ate none thereafter. On d 1 of the aster trial, cattle rapidly ingested 95% of the aster collections, which provided an average Se dose to each steer of 2.85 ± 0.2 mg Se/kg BW. The following day the cattle showed visible inappetence and lethargy.
Sheep consumed a small amount of western aster on d 1 and 2 of the trial (9 and 16% of the amount offered, respectively), but most of that consumption was by 2 animals; overall, consumption declined to <2% of offered material during the last 2 d of the trial. Sheep consumed an average of about 0.75 mg Se/kg BW on d 1 and 2 of the aster trial and a very small amount of Se on d 3 and 4.

Selenium Preference Trials with Pelleted Forage of Varying Selenium Concentration

**Trial 1.** The first trial was 5 d, and control and 5, 25, 45, and 110 mg/kg Se pellets were used for the treatments. There was a day × treatment interaction ($P < 0.006$) for cattle. Consumption of the control pellet by cattle was greater on all trial days compared with all other Se pellets ($P < 0.001$). On d 1 and 2 consumption by cattle of the 5, 25, 45, and 110 mg/kg Se pellets did not differ ($P > 0.57$) whereas cattle ate more ($P < 0.001$) of the 5 mg/kg Se pellet than the higher Se pellets (25, 45, and 110 mg/kg Se) on d 3, 4, and 5. Consumption by cattle of the 25, 45, and 110 mg/kg Se pellets did not differ on d 3, 4, and 5 ($P \geq 0.12$). There were differences among days for both Se intake (mg/kg BW; $P = 0.001$) and pellet intake (% of BW; $P = 0.02$). Selenium intake was greatest on d 1 and then decreased over the next 4 d (Fig. 6B) whereas pellet intake decreased on d 2 relative to d 1, 4, and 5 (Fig. 6B).

**Trial 2.** The second trial was 4 d, and control and 25, 45, and 110 mg/kg Se pellets were used for the treatments. There were no day × treatment interactions for cattle or sheep ($P \geq 0.38$), but there were treatment effects for both ($P < 0.0001$). Cattle consumed more ($P < 0.0001$) of the control pellet than the 25, 45, and 110 mg/kg Se pellets (Fig. 7A). Similarly, cattle consumed more ($P < 0.0001$) of the 25 mg/kg pellet than the 45 and 110 mg/kg Se pellets. There were no differences ($P > 0.88$) in cattle consumption of the 45 and 110 mg/kg Se pellets. There were differences among days for both Se intake (mg/kg BW; $P < 0.0001$) and pellet intake (% of BW; $P = 0.04$). Selenium intake was greatest on d 1 and then decreased over the next 2 d (Fig. 7B) whereas pellet intake decreased on d 2 but began to rebound on d 3 and continued to increase on d 4 (Fig. 7B).

Sheep consumed more ($P < 0.0001$) of the control pellet than the 25, 45, and 110 mg/kg Se pellets (Fig. 8A).
However, consumption of the 25, 45, and 110 mg/kg Se pellets did not differ \( (P \geq 0.36) \) even though numerically sheep consumed much more of the 110 mg/kg Se pellet early in the trial. Variability among sheep was high as 2 sheep initially consumed the 110 mg/kg Se pellet and then their consumption of the 110 mg/kg Se pellet declined. Two other sheep ate little or none of the 110 mg/kg Se pellet. There were no differences \( (P = 0.35) \) among days for Se intake (mg/kg BW; Fig. 8B), but there was a trend \( (P = 0.10) \) towards decreasing pellet intake (% of BW) over time. The lack of differences was primarily due to the large variation in response to Se among sheep.

**Trial 3.** The third trial was 3 d, and control and 45 and 110 mg/kg Se pellets were used for the treatments. There was a day × treatment interaction \( (P < 0.0003) \) for cattle consumption of pellets (Fig. 9A). With one exception, cattle consumption of the control and 45 and 110 mg/kg Se pellets differed \( (P < 0.001) \) from one another each day. The lone exception was that there was no difference \( (P > 0.95) \) in cattle consumption of the 5 mg/kg Se pellet compared with the 5 and 45 mg/kg Se pellets \( (P < 0.001) \) on d 2. On d 3 consumption by sheep of the 5, 25, 45, and 110 mg/kg Se pellets did not differ \( (P > 0.57) \) whereas cattle ate more \( (P < 0.001) \) of the 5 mg/kg Se pellet than the higher Se pellets (25, 45, and 110 mg/kg Se) on d 3, 4, and 5. Consumption of the 25, 45, and 110 mg/kg Se pellets by cattle did not differ on d 3, 4, and 5 \( (P \geq 0.12) \). For intake of Se (mg/kg BW) and for pellet intake (% of BW), day means with different letters differ \( (P < 0.05) \). Error bars represent SEM values.
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There were no differences among days for both Se intake (mg/kg BW; \( P = 0.04 \)) and pellet intake (% of BW; \( P = 0.42 \)) and pellet intake (% of BW; \( P = 0.90 \); Fig. 10B).

DISCUSSION

Grazing animals occasionally ingest large and fatal amounts of seleniferous plants (Fessler et al., 2003; Davis et al., 2012). More typically, anecdotal information suggests that they do not consume substantial amounts of plants with high Se concentrations (Beath, 1920; Davis et al., 2000; Burrows and Tyrl, 2001) because of the taste or odor. However, initial forage selection by cattle and sheep was not influenced by Se concentration, even when plant concentrations exceeded 5,000 mg/kg Se as in the initial presentation of the western aster. All the animals in this study were naïve to high-Se forages at the beginning of the study. It was only when animals may have experienced negative postingestive effects from consuming Se-accumulator forage that there was an alteration in forage preference (Provenza, 1995). For example, cattle consumed about 2.85 mg Se/kg BW within a few minutes on d 1 of the western aster trial in phase I. Sodium selenite dosed to sheep above 2 mg Se/kg BW resulted in tachypnea and respiratory distress (Tiwary et al., 2006). The Se forms most common in Se accumulator plants are selenate and Se-methylselenocysteine, both of which may be more bioavailable and lead to greater toxicity than selenite (Davis et al., 2013). On d 2 of the aster trial in the first portion of this study, the cattle were listless and showed inappetance. The cattle apparently did not consume sufficient Se in the grass or alfalfa trials to experience adverse postingestive consequences.

Consumption of fresh aster was initially lower by sheep relative to the grass and alfalfa. Cattle consumed
virtually all of the fresh aster on d 1 of the trial but none thereafter. As with alfalfa and the grass, there was no evidence of Se concentration affecting the initial selection. However, even though there was no initial relationship between aster consumption and Se concentration by cattle on d 1, the consumption of the aster on d 1 apparently caused a strong conditioned food aversion to the western aster, as cattle did not eat any aster on d 2 to 4. This aversion was likely caused by the negative postingestive effects of the high Se concentration in some of the western aster collections. Pfister et al. (2010) found that Se from aster dosed to sheep at 3 mg/kg BW conditioned a strong taste aversion to a palatable food. Cattle may have been generalizing a taste aversion based on shared flavors in the low- and high-Se asters, as they ate none of the low Se aster after d 1. Sheep consumption of aster appeared to be random with regard to Se, as they consumed mostly the highest Se collections on the first day, some low and high Se aster on d 2, and then consumption decreased to almost nil on the last 2 d. Unlike cattle, sheep did not show a total aversion to all the aster collections after the first exposure, but the decrease in consumption on the final 2 trial days may have reflected a weaker and delayed aversion from consumption during the first 2 d.

Selenium concentration in blood or tissues is not tightly regulated in livestock (Underwood and Suttle, 1999), and therefore there may be a substantial time lag between dietary Se concentrations resulting in deficiency or chronic (but not acute) toxicity. Both sheep and cattle began these trials with slightly lower than normal Se concentrations in their whole blood. The influence of their initial Se status on animal preferences for the fresh forages differing in Se concentration is unknown. Sheep had whole blood Se concentrations that peaked at the end of the study at >0.8 mg/kg, and some individual sheep showed intermittent clinical signs of inappetence and depression during the preference trials. However, variability in sheep response to Se was substantial, as
some sheep were apparently impacted to a lesser degree from eating Se pellets. Morrow (1968) also reported that sheep varied widely in their susceptibility to sodium selenite dosed orally.

Cattle showed mild clinical signs the day after ingesting fresh western aster but no clinical signs of Se toxicity during the preference trials. Whole blood Se concentrations in cattle 48 h after consumption of the western aster (Se dose of 2.85 mg Se/kg BW) averaged about 0.5 mg/kg Se, up from 0.25 mg/kg Se. In the same region where the western aster was collected for this study, 16 steers were fatally poisoned by western aster in 2009 (Davis et al., 2012). Sampling from this acute intoxication episode showed that 9 surviving steers had blood Se concentrations in excess of 1 mg/kg Se at 14 d postexposure (Davis et al., 2012) and had blood Se concentrations near 0.5 mg/kg at 90 d postexposure.

The low-Se aster preference trial demonstrated that sheep were not negatively influenced by western aster used with alfalfa to make pellets. This trial lends support for the effects of Se alone on food intake in the preference trials with pellets varying in Se concentration. In the latter trials, cattle and sheep ate substantial amounts of the pellets with the lowest available concentration of Se in the trial (i.e., 5, 25, or 45 mg/kg) at times. Because the amount of the control pellets offered was about 50% of normal daily feed intake (i.e., 1.5% of BW), cattle and sheep could reach satiety only by consuming some of the pellets with higher Se concentrations. Indeed, in each of the pellet trials, the highest consumption of total Se was on d 1 and then with negative postingestive feedback the animals would greatly reduce the amount of Se they ate over the remaining days of the trials by selecting the pellets with the lowest Se concentrations. Indeed, in each of the pellet trials, the highest consumption of total Se was on d 1 and then with negative postingestive feedback the animals would greatly reduce the amount of Se they ate over the remaining days of the trials by selecting the pellets with the lowest Se concentrations. Cattle maintained their total pellet intake between 2 and 3% BW during all the Se-preference trials even though they showed a modest decrease and then a rebound in total intake after d 1 of Trials 1 and 2. In all 3 of the Se-preference trials, total pellet intake by cattle mirrored the amount of Se (mg/kg BW) they ingested.

The threshold at which cattle and sheep consumed pellets with higher Se concentrations changed as the animals’ choices were restricted during the progression of Trials 1, 2, and 3. There was an apparent interaction between animals’ hunger and the negative feedback from eating the higher Se pellets. In Trial 1, with 5 choices, cattle ate a substantial amount of the 5 mg/kg Se pellet and some of the 25 mg/kg Se pellet over the 5 d. When the 5 mg/kg Se pellet was removed for Trial 2, cattle ate a substantial amount of the 25 mg/kg Se pellet. When the 25 mg/kg Se pellet was removed for Trial 3 with 3 choices, cattle ate substantial but declining quantities of the 45 mg/kg Se pellet.

For sheep, the results were more complex, as sheep ate substantial quantities of the control pellet, the 5 mg/kg Se pellet, and the 110 mg/kg Se pellet initially on d 1 of Trial 1 (5 choices; about 4% of BW in total pellet intake), but intakes declined greatly on d 2 and rebounded on the last 3 trial days. Sheep were apparently responding to the initial Se intake and then selected pellets with relatively lower Se concentrations. Although there was no treatment × day interaction, apparently from the high variability, sheep initially ate substantial amounts of the 110 mg/kg Se pellet during Trial 2 (4 choices) after the removal of the 5 mg/kg Se pellet. Apparently the consumption of the 110 mg/kg Se pellet on d 1 led to reduced consumption of the 110 mg/kg Se pellet on subsequent days. During Trial 2 (4 choices), total consumption of pellets by sheep closely mirrored the amount of Se ingested. During Trial 3, sheep intake of Se was highest on d 1 as sheep ate all 3 pellet choices, with a substantial decline in Se intake on subsequent days. However, by selecting only the control and 45 mg/kg Se pellets on the final 2 trial d, sheep were able to maintain total pellet intake at or above 2% of BW.

Grazing herbivores face a number of challenges when grazing on rangelands with toxic plants (Laun-baugh et al., 1993), and those challenges are exacerbated when grazing on rangelands with seleniferous soils that produce a tremendous mosaic of variability in plant Se concentrations. Both the toxicity and nutrient value will differ among plant species and vary greatly in time (i.e., plant phenology) and space. For example, Davis et al. (2012) reported that Se concentrations exceeded 4,000 mg/kg in western aster in 1 location but within 50 m, Se concentrations in the same plants were <15 mg/kg. Day-to-day shifts in forage and pellet consumption indicate that cattle and sheep avoid excessive Se intake. These findings support previously published statements that herbivores use a number of interrelated behavioral and physiological strategies to reduce the risk of poisoning, including avoiding or reducing toxin intake through changes in intake and diet selection (Provenza et al., 1992; Pfister, 1999; Iason and Villalba, 2006). When grazing animals alter consumption of toxic plants in favor of less toxic or nontoxic plants, learning is usually involved (Provenza, 1995, 1996). Herbivores identify toxic plants by associating the flavor of the plant (taste and smell) to postingestive consequences (Garcia, 1989; Provenza, 1995). It was clear in this study that high Se concentrations in fresh forages had no effect on initial consumption by cattle or sheep. When given Se pellets, initial responses were variable and then animals appeared to adjust their food intake according to the level of Se in the forage. Behavioral adjustments by grazing livestock may greatly reduce toxin intake (Provenza et al., 1992), including consumption of Se-accumulating plants. If alternative forages are available and a nonle-
thal initial Se dose is consumed, animals may be initially averted to Se-accumulator plants and avoid consumption in subsequent encounters. However, if grazing animals are not averted and do not subsequently avoid high-Se plants, there remains the potential for toxicity.

LITERATURE CITED


