Rangeland Ecology & Management 70 (2017) 380–387

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Original Research

Effects Energy Supplementation and Time on Use of Medusahead by Grazing Ewes and Their Lambs☆

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ARTICLE INFO

Article history:
Received 23 April 2016
Received in revised form 29 November 2016
Accepted 30 November 2016

Keywords:
diet selection
foraging behavior
preference
weed control

ABSTRACT

Medusahead is an annual weed that invades millions of acres in the western United States. This study explored the effect of energy supplementation on use of this unpalatable weed by ewes and their lambs. Thirty-six ewes with their lambs (2 − 3 mo old) were randomly assigned to 12 groups (3 ewes with their lambs per group), and half of the groups received 2.5 kg group d^{-1} of an energy-based supplement (beet pulp − barley − Ca-propionate, 66:30:4; as-fed basis). After supplementation, all groups grazed plots with medusahead infestation for 15 d. Lambs were then weaned, kept in the same groups but without supplementation, and allowed to graze medusahead-infested plots for 3 d. Grazing events were recorded daily at 5-min intervals, and defoliation of medusahead tillers was measured in all plots. The proportion of grazing events recorded on medusahead and the proportion of defoliated medusahead tillers were not affected by supplementation in either ewes or lambs ($P > 0.05$). All ewe-lamb groups presented a greater proportion of medusahead use during the second half of the grazing period ($P < 0.05$). Nevertheless, the average proportion of events recorded for medusahead use was never greater than 7%, which was similar to the relative availability of medusahead in the community (i.e., 6%). Use of medusahead by ewes was correlated with that observed for their lambs ($r = 0.83$; $P < 0.05$), and weaned lambs showed a similar proportion of grazing events on medusahead to those observed before weaning ($P > 0.05$). These results suggest that mothers influence medusahead use by their offspring. They also suggest that despite the low palatability of medusahead, sheep will not avoid medusahead when grazing moderately infested rangeland. The diversity of the plant community likely contributed to this outcome, which might have also reduced the impact of the supplement on medusahead use by sheep.

Introduction

Medusahead (*Taeniatherium caput-medusae* subsp. *asperum*) is a Eurasian annual grass that has invaded > 10 million ha of rangeland in the Pacific Northwest, California, Utah, and Nevada (Johnson and Davies, 2012). Grazing represents a sustainable and low-input method for weed control. In fact, stakeholders, scientists, and land managers see high potential for the use of grazing as a tool to control medusahead in western rangelands (James et al., 2015). Nevertheless, livestock have reportedly displayed remarkably low preference for medusahead during grazing, attributed to the low nutritional value and high silica content of the weed (Lusk et al., 1961; George et al., 1989; Young, 1992). In turn, medusahead avoidance increases grazing pressure on palatable native plants, which further reduces animal carrying capacity and contributes to the spread of the weed (Hironaka, 1961; Torrel et al., 1961).

Paradigms on foraging behavior emphasize the importance of positive experiences early in life with the biochemical context (provided by the plant community or supplements) on preference for target feeds (Villalba et al., 2015). Preference for a particular feed depends on not only its intrinsic (i.e., nutritional, toxicologic) properties but also the nutritional context where that food is ingested. An instance of this type of phenomenon is called the *induction effect,* which consists of an increased intake of an unpalatable food when it is associated with the ingestion of a preferred food in a sequence familiar to the animal (Flaherty, 1996; Provenza et al., 2003). Caton and Dhuyvetter (1997) and Garcés-Yépez et al. (1997) reported that concentrates containing highly digestible fiber (i.e., beet pulp) increase intake of low-quality forages by livestock because such supplements maintain a favorable rumen environment (i.e., pH and digestible fiber). Thus, conditioning animals with appropriate supplemental feeds may lead to a more even utilization of palatable and unpalatable resources in a plant community and, as a consequence, to the maintenance of biodiversity in the landscape (Provenza et al., 2003; Baraza et al., 2005).

In addition to the nutritional context, positive experiences early in life with the mother can have lifelong influences on herbivores by causing neurologic, morphologic, and physiologic changes that influence

☆ This research was supported by grants from the National Institute of Food and Agriculture, US Department of Agriculture (agreement no. 2009-35101-05360).

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http://dx.doi.org/10.1016/j.rama.2016.11.005
1550-7424/

foraging behavior (Provenza and Balph, 1990; Distel et al., 1994, 1996). Given the appropriate nutritional context at an early stage of development, animals may increase consumption of medusahead and its use may persist throughout the lifetime of the individual.

We hypothesized that the use of an energy supplement would enhance intake of and preference for medusahead by sheep and that this effect would transmit from mother to offspring. To test this hypothesis, we determined the influence of an energy-based supplement on use of medusahead by ewes and their lambs and the subsequent use of the weed by weaned lambs.

Material and methods

Study Site

The experiment was conducted on privately owned land with medusahead infestation in Mantua, Box Elder County, Utah, United States (41°29′51″N and 111°56′32″W). The ecological site is Mountain Stony Loam (Wadman, 2012), which is located between 1670 and 2560 masl and has slopes between 5% and 70%. The soils transitioned from the Goring-Yeates Hollow association, on alluvium and colluvium derived from quartzite and sandstone at the lowest slope position, to the Agassiz-Picayune association at the highest slope positions, composed of colluvium and limestone residuum. The soils were Xerolls with a well-developed organic-rich A-horizon. They had a stony, cobbly, or gravelly loam texture upslope and clayey texture downslope, with moderate permeability and moderate erosivity. Upslope soils tended to be shallower and drier.

Cold snowy winters and cool dry summers characterize the climate. The plant community is Mountain Big Sagebrush with introduced non-native plant species (Wadman, 2012). The functional group of grasses is composed of mainly *Elymus trachycaulus, Poa secunda, Poa bulbosa, Poa fendleriana,* and *Leymus cinereus*. Some representative forbs are *Achillea millefolium* L., *Balsamorhiza sagittata* (Pursh) Nutt., *Lupinus caudatus* L., and *Crepis acuminata* L. The dominant shrubs are *Artemisia tridentata* Nutt. subsp. *vaseyana*. Non-native grasses are medusahead and *Bromus tectorum* L. Identification of plant species was made with support of Natural Resources Herbarium collection, Utah State University (USU).

Grazing Blocks

Six 0.18-ha blocks, each divided into 2 plots (0.09 ha plot^{-1}), were marked at the study site in order to evaluate the effect of an energy-rich supplement on use of medusahead by ewes and their lambs. Each plot was delimited using electric fence, and a pen of ~3.0 m^2 was assembled outside each plot for overnight enclosure of the animals. Culinary water, salt (White Salt Block, North American Salt Company, Overland Park, KS), and trace-mineralized salt blocks (Morton iOfixt T-M, Chicago, IL) were provided in ad libitum amounts inside each pen throughout the study. Three control plots (no grazing) were randomly located between the grazed blocks.

In order to test for the effects of exposure with their mothers to a supplement on medusahead use by weaned lambs, six 0.021-ha blocks, each divided into 2 plots (0.0105 ha plot^{-1}) were marked on the study site with outside pens and fenced as described earlier. Blocks were assembled 50 m to the northeast of the blocks that were grazed by ewes and their lambs.

Effect of Supplementation on Medusahead Use by Ewes and Their Lambs

Experimental Design

The study was conducted according to procedures approved by the Utah State University Institutional Animal Care and Use Committee (Approval #1551). Thirty-six crossbreed ewes with their lambs (2 − 3 months of age) grazed an orchardgrass *(Dactylis glomerata)* pasture at the Green Canyon Ecology Center, USU, Logan, Utah, during May 2013. All animals were also fed ~8 kg d^{-1} of an energy-based supplement from 7 May to 31 May 2013, in order to familiarize the animals with this feed before they grazed medusahead-infested rangeland. The energy supplement was a mixture of beet pulp, barley, and Ca-propionate (Sigma-Aldrich, St. Louis, MO) at a rate of 66:30:4 (as-fed basis).

Twenty-three ewes had single lambs, and 13 ewes had twins. The average initial body weight (BW) of ewes and lambs was 72.4 ± 8.3 and 25.0 ± 8.9 kg, respectively. All animals were transported to the study site on 1 June 2013.

Within each of the six 0.18-ha experimental blocks described in the section of *Grazing plots*, one group of three ewes with their lambs (3.8 ± 0.8 lambs group^{-1}) received the energy supplement (Supplemented groups) and grazed in one of the 0.09-ha plots of the block, whereas another group of three ewes and lambs (4.3 ± 1.0 lambs group^{-1}) did not receive a supplement (Nonsupplemented groups) and grazed on the other 0.09-ha plot of the block. Each supplemented group received 2.5 kg of the supplement (94% dry matter [DM]) from 0750 to 0830 daily. Supplement intake ranged from 1.8 to 2.3 kg DM d^{-1}. The supplement's chemical composition is shown in Table 1. All ewes and their lambs were released to graze their respective plots from 0830 to 1700, when all animals were penned overnight. Sheep grazed for 15 consecutive days (from 2 to 16 June 2013). Medusahead was in the late vegetative stage at the beginning of the experiment and in the late reproductive stage toward the end of the experiment.

Scan Sampling

Behavior of ewes and their lambs was recorded at 5-min intervals from 0830 to 1100 and from 1600 to 1700 using the scan sampling technique (Altman, 1974). Foraging activities involved those events when animals were observed grazing medusahead and other functional groups (annual grasses other than medusahead, bunch grasses, and forbs) in the plant community; additional behaviors were walking, resting, ruminating, nursing, and drinking. Observations were made in three blocks per day during alternate days: three randomly selected blocks were scanned by three observers on days 1, 3, 6, 8, 11, and 13, whereas the remaining three blocks were scanned on days 2, 4, 7, 9, 12, and 14. The proportion of grazing events on medusahead and other functional groups in the plant community relative to the total number of scans recorded per day (3.5 h) was determined.

Evaluation of the plant community

Plant biomass production was estimated pregrazing and postgrazing in all grazed and ungrazed plots using a rising plate meter (Michell, 1982), 0.0985 m^2 plate^{-1}. The relative abundance of medusahead and different plant functional groups (forbs, bunch grasses, and annual grasses other than medusahead) on a wet basis (WB) were visually estimated pregrazing and postgrazing in 25 squares (0.0985 m^2 square^{-1}) randomly distributed within a zig-zag transect. These visual estimations were made in a randomly selected plot per block, with the restriction that three plots were grazed by supplemented sheep and three plots were grazed by nonsupplemented sheep. Shrubs occurred in low frequency in all plots (<2% of frequency), and their abundance was thus not considered in the study.

Four squares (0.0985 m^2 square^{-1}) within the aforementioned transect were randomly selected and harvested at the ground level. Plant material was taken to the laboratory, manually sorted into medusahead and plant functional groups, and weighed on a WB. This information was used to calculate the percentage of medusahead and functional groups present in each sample (WB), and these values were compared with the relative abundance estimated visually (WB) in the plots. This was done to test how reliable the visual estimations were.

Samples of supplement, medusahead, and functional groups were dried in a forced air oven at 60°C until constant weight to estimate DM content. A composite of medusahead and each plant functional

Table 1
Chemical composition of the energy supplement and of medusahead and functional groups in the plant community where ewes and their lambs grazed during the study.

Feed resource	Content (g kg^{-1} dry matter)				
	Crude protein	Neutral detergent fiber	Acid detergent fiber	Ash	Acid insoluble ash
Energy supplement[1]	105.9	320.1	166.5	93.1	22.9
Plant community in rangeland plots (mean ± SEM)[2]					
Pregrazing					
P value	<0.01	<0.01	<0.01	<0.01	<0.01
Medusahead	171.9 ± 8.5[a]	546.7 ± 5.6[a]	247.3 ± 1.9[a]	127.3 ± 2.9[a]	68.3 ± 2.0[a]
Other annual grasses	117.2 ± 4.9[b]	595.9 ± 1.1[b]	290.8 ± 2.0[b]	87.5 ± 4.8[bc]	40.9 ± 1.6[b]
Bunch grasses	95.3 ± 1.4[c]	584.1 ± 7.8[b]	288.1 ± 4.6[b]	82.8 ± 3.0[b]	42.6 ± 1.2[b]
Forbs	153.5 ± 20.2[ab]	345.9 ± 14.7[c]	233.5 ± 11.6[a]	110.2 ± 9.9[ac]	18.8 ± 4.6[c]
Postgrazing					
Medusahead	84.2 ± 3.5	653.4 ± 4.0	329.6 ± 9.7	107.3 ± 6.0	78.7 ± 7.4
Other annual grasses	83.5[1]	655.6[1]	339.0[1]	NA	NA
Bunch grasses	19.3 ± 0.0	718.9 ± 4.6	407.1 ± 5.6	NA	NA
Forbs	9.2 ± 1.2	383.3 ± 29.7	275.2 ± 23.0	98.5 ± 2.5	4.9 ± 0.5

Same superscript into column of pregrazing means no difference ($P > 0.05$).
Acid insoluble ash represents >90% silica (Charca et al., 2007).
NA, not analyzed for insufficient sample.
[1] Chemical analyses of 1 replicate.
[2] Chemical analyses of 3 spatial replicates.

group was formed with samples from two blocks. Samples were ground using a Wiley Mill (Thomas Scientific, Swedesboro, NJ) with a 1-mm screen for chemical analyses.

The available DM biomass (pregrazing and postgrazing; Eq. (1)), the amount of DM biomass harvested by sheep (pregrazing biomass [kg DM plot^{-1}] – postgrazing biomass [kg DM plot^{-1}]), and the percentage of relative frequency (Eq. (2)) for medusahead and each functional group were calculated per plot.

$$\mathrm{AB}\left(\mathrm{kg\ DM\ plot}^{-1}\right) = \frac{\dfrac{\mathrm{RA}\ (\%) \times \mathrm{TAB}\left(\mathrm{kg\ WB\ plot}^{-1}\right)}{100} \times \mathrm{DM}\ (\%)}{100} \quad (1)$$

$$\mathrm{RF}\ (\%) = \frac{\mathrm{NS}}{\mathrm{TNS}} \times 100 \quad (2)$$

where *AB* is the available biomass of medusahead or each functional group, *DM* is dry matter, *RA* is the relative abundance of medusahead or functional group on wet basis, *TAB* is the total available biomass on wet basis, *WB* is wet basis, *RF* is the relative frequency, *NS* is the number of squares with medusahead or functional group, and *TNS* is the total number of squares.

Proportion of Medusahead Defoliation

Squares (90.2 cm^2 square^{-1}) containing medusahead tillers on each grazed and ungrazed plot were marked using flagging tape, which was anchored to the soil with nails at each corner of the square. This procedure is a modification of the technique described by O'Reagain and Grau (1995) to assess defoliation on bunch grasses. The number of squares was similar between plots within the same block. However, the number of squares across blocks varied between 5 and 15, as it was proportional to the spatial distribution and abundance of medusahead within each of the blocks.

Medusahead cover in each square was visually ranked from 1 to 5 according to the percentage of soil covered by medusahead tillers: 1 = 10% cover (9.0 cm^2), 2 = 30% cover (27.1 cm^2), 3 = 50% cover (45.1 cm^2), 4 = 70% cover (63.2 cm^2), and 5 = 90% cover (81.2 cm^2). Medusahead tillers within each square were similar in height, and the height of the tallest leaf in the tillers was measured in cm. The soil area (cm^2) covered by (according to the assigned rank) and the height (cm) of medusahead were used to estimate the initial volume of the biomass (IV, cm^3) contained inside the squares before grazing. Defoliation of medusahead tillers was measured on days 5, 10, and 15 of the experiment. The volume of biomass of the defoliated tillers were calculated (Eq. (3)) inside each marked medusahead square:

$$\mathrm{DTV}\ \left(\mathrm{cm}^3\right) = \mathrm{IV}\left(\mathrm{cm}^3\right) - \left(\mathrm{AMT}\left[\mathrm{cm}^2\right] \times \mathrm{AH}[\mathrm{cm}]\right) \quad (3)$$

where *DTV* is the defoliated tiller volume into marked medusahead square; *IV* is the initial volume of medusahead biomass into marked squares; *AMT* is the area of medusahead tillers, according to the rank of soil covered by medusahead tillers; and *AH* is the average height of the defoliated leaves remaining on the tillers after grazing period. Finally, the proportion of medusahead volume removed by sheep was calculated (DTV [cm^3]/IV [cm^3]). The height of medusahead plants that did not receive defoliation after grazing was used to correct for the initial volume of medusahead biomass since medusahead plants grew in height during grazing.

Effect of Supplementation on Medusahead Use After Weaning

Lambs were weaned on 17 June and kept in the same groups that grazed with their mothers. Groups of lambs were housed in their respective pens (~3.0 m^2) outside their grazing plots and fed ad libitum amounts of alfalfa pellets for 4 days. Ewes were moved back to the Green Canyon Ecology Center and weighed to calculate the average daily BW change.

Lamb groups grazed their respective 0.0105-ha plots (see *Grazing blocks*) without supplementation from 0830 to 1700 for 3 consecutive days (21 − 23 June). Lambs depleted > 90% of the available plant biomass in all plots after 3 days of grazing, and at this time medusahead was in the late reproductive stage. Thus, animals were removed from the plots after 3 days of grazing.

The proportion of grazing events on medusahead and other functional groups in the plant community by lambs was determined, as was described in the section of *Scan sampling* for grazing ewes with their lambs, on 21 and 22 June. Three randomly selected blocks were scanned each day by the observers.

The biomass production was estimated pregrazing and postgrazing using a rising plate meter (Michell, 1982), 0.0985 m^2 plate^{-1}. The relative abundance of medusahead and plant functional groups were estimated (WB) in each plot by visual inspection of the whole plot by two observers pregrazing and postgrazing.

Four squares (90.2 cm^2 square^{-1}) containing medusahead tillers were marked and assessed before and after grazing in each plot as described earlier in the *Proportion of medusahead defoliation* section. Lambs were moved to the Green Canyon Ecology Center on 24 June and weighed to calculate the average daily BW change.

Chemical Analyses

The energy supplement and spatial replicates of medusahead, annual grasses other than medusahead, bunch grasses, and forbs pregrazing and postgrazing were analyzed for crude protein (CP), neutral (NDF) and acid (ADF) detergent fiber, ash, and acid insoluble ash (AIA). CP was calculated by measuring nitrogen content (Wiles et al., 1998) and then by multiplying this content by 6.25. NDF and ADF were measured according to Van Soest et al. (1991); ADF measure was sequential of NDF. Ash content was obtained by burning samples at 550°C for 6 h (Allen, 1989). AIA is an approximation of silica content (i.e., >90% of AIA is silica [Charca et al., 2007]), and it was determined by the method of 2*N* HCl (Van Keulen and Young, 1977).

Statistical Analyses

Analyses were computed using SAS (SAS Institute, Inc., Cary, NC; Version 9.1 for Windows). The covariance matrix structure used was the one that yielded the lowest Akaike information criterion. The model diagnostics included testing for a normal distribution and homoscedasticity. Data were transformed when needed according to the Box-Cox method, but nontransformed means ± SEM are reported. Means were analyzed using Tukey's multiple comparison tests when *F*-ratios were significant ($P < 0.05$). A tendency was considered when $0.05 < P < 0.15$.

The correlation coefficient between relative abundance of medusahead and plant functional groups determined by visual estimation and by weight on a WB was determined.

The proportion of events recorded for total grazing events and eating medusahead, annual grasses, bunch grasses, and forbs across the 3.5 h of daily observations, as well as the proportion of medusahead volume removed during grazing by ewes with their lambs, were analyzed as mixed-model effects with block as random effect and animal (ewe, lamb), supplement (yes, no), and day as fixed factors.

For weaned lambs, block was the random effect and previous exposure to supplement (yes, no) was the fixed factor. In order to assess differences in medusahead use by lambs before and after weaning, the proportion of events recorded for grazing medusahead by lambs (before and after weaning) was analyzed using a 1-way analysis of variance with day as the fixed factor.

The relationship between ewes and their respective lambs for the proportion of grazing events (total grazing events, and grazing events recorded on medusahead, other annual grasses, bunch grasses, and forbs) was estimated by the coefficient of correlation for those events, where each ewe and its offspring (an average of grazing events for twins) were considered a replicate.

Average daily weight gain for ewes and lambs was analyzed as a 1-way analysis of covariance with supplement (yes, no) as a fixed factor and the initial body weight as a covariate. The biomass (DM) removed during grazing by supplemented and nonsupplemented sheep was analyzed as a 1-way analysis of covariance, with block as covariate and supplement (yes, no) as fixed factors. Content of CP, NDF, ADF, ash, and AIA in the pregrazing forages was analyzed using a 1-way analysis of variance with forage as the main factor.

Results

Effect of Supplement on Medusahead Use by Ewes and Their Lambs

Chemical Composition of the Plant Community

Medusahead and plant functional groups showed differences in their chemical composition at the beginning of the grazing period (Table 1). Medusahead presented more desirable nutritional qualities than other grasses, except for the greatest AIA content. Toward the end of the grazing period, annual grasses (including medusahead) had more desirable nutritional qualities than bunch grasses (see Table 1). Plant chemical quality decreased as the season progressed (see Table 1).

Scan Sampling

Supplementation did not have an effect on the proportion of total grazing events recorded ($P = 0.69$) or the use of medusahead ($P = 0.89$) or other functional plant groups ($P \geq 0.31$) in the plant community.

Ewes and their offspring did not differ in the average proportion of total grazing events ($P = 0.70$). However, ewes grazed forbs to a greater extent than did lambs: 0.15 ± 0.02 versus 0.11 ± 0.02 proportion of scans, respectively ($P = 0.03$). In contrast, lambs tended to display a greater proportion of grazing events on bunch grasses than ewes, 0.42 ± 0.03 versus 0.38 ± 0.04, respectively ($P = 0.07$). No differences between ewes and lambs were detected for the proportion of events recorded for eating medusahead ($P = 0.54$) or other annual grasses ($P = 0.84$).

Across days, the proportions of total grazing events (Fig. 1**A**) and for eating bunch grasses (Fig. 1**B**) presented cyclic patterns. While the proportion of events recorded for grazing forbs (Fig. 1**C**) and medusahead increased across time (Fig. 1**D**). Annual grasses other than medusahead tended to be used to a greater extent during the first days than toward the end of the trial ($P = 0.10$). The average daily proportion was from 0.014 ± 0.005 to 0.005 ± 0.002.

In general, there was significant correlation between ewes and their lambs in the use of the different plant functional groups (Table 2). The correlation between mothers and their offspring for grazing medusahead was high and equal for supplemented and nonsupplemented animals.

Evaluation of the Plant Community

The average available biomass in the plots grazed by supplemented ewes and their lambs pregrazing and postgrazing was 321.7 ± 18.3 and 132.0 ± 30.9 kg DM plot^{-1} (plot = 0.09 ha), respectively. For the plots grazed by nonsupplemented ewes and their lambs, the average available biomass pregrazing and postgrazing was 289.4 ± 5.4 and 139.3 ± 22.9 kg DM plot^{-1}, respectively. The amount of biomass removed by different groups was not affected by supplementation ($P = 0.35$). Biomass production in the ungrazed plots increased from 282.5 ± 6.0 to 496.2 ± 55.3 kg DM plot^{-1}.

The percentages of relative abundance (WB) of medusahead, other annual grasses, bunch grasses, and forbs estimated visually in the plots (11.0 ± 3.4%, 5.2 ± 1.8%, 22.7 ± 3.8%, and 61.0 ± 4.6% WB, respectively) versus percentages of relative abundance estimated by weight (WB) (11.5 ± 3.7%, 3.8 ± 1.1%, 26.2 ± 4.0%, and 58.5 ± 4.8% WB, respectively) showed the following correlation coefficients ($P < 0.0001$): 0.92, 0.74, 0.84, and 0.85, respectively. The most abundant resources into the plots were forbs and bunch grasses (Table 3). The relative abundance of medusahead increased after grazing (see Table 3).

Based on the composition of the removed biomass in the plots (see Table 3), the diet of supplemented sheep was composed of 4.0 ± 1.9% medusahead, 9.0 ± 0.9% other annual grasses, 39.0 ± 4.6% bunch grasses, and 48.1 ± 3.4% forbs, whereas the diet of nonsupplemented sheep was composed of 2.3 ± 1.1% medusahead, 25.7 ± 6.3% other annual grasses, 41.5 ± 4.9% bunch grasses, and 30.6 ± 3.9% forbs.

During the grazing period, ewes and their lambs harvested different percentages of the initial biomass available in the plots (DM basis): < 50% of medusahead, ~15% of other annual grasses, < 33% of bunch grasses, and < 53% of forbs. The relative frequency of medusahead increased throughout grazing period, being the opposite for the rest of the functional plant groups (see Table 3).

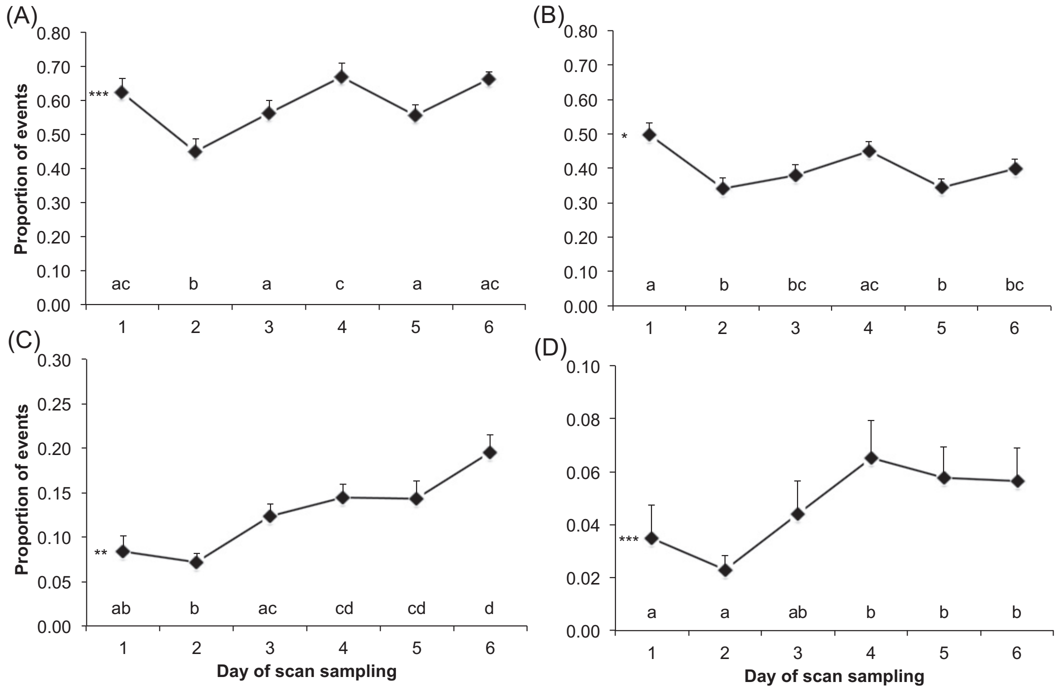

Figure 1. Daily average proportion of grazing events displayed by sheep groups (ewes and their lambs) grazing medusahead-infested rangeland plots for 6 days of scan sampling. Grazing events were recorded from 0830 to 1100 and from 1600 to 1700. Grazing event: **A,** total; **B,** bunch grasses; **C,** forbs; **D,** medusahead. Vertical bars represent the standard errors of measurement. * $P < 0.05$; ** $P < 0.01$; and *** $P < 0.0001$. For each day, the average proportion of events with the same letter did not differ ($P > 0.05$).

Medusahead Defoliation

Supplementation had no effect on defoliation of medusahead tillers ($P = 0.30$). However, sheep defoliated different proportions of medusahead across time ($P = 0.0013$; Fig. 2); they removed more medusahead volume in the first 10 days. Supplement and day interaction did not have an effect ($P = 0.57$).

Effect of Supplementation on Medusahead Use After Weaning

Scan Sampling

Lambs previously supplemented with their mothers tended to show a lower proportion of total grazing events than nonsupplemented lambs ($P = 0.09$; Fig. 3). Prior exposure to supplementation did not have an effect on grazing events recorded on medusahead or on other functional groups in the plant community ($P > 0.05$; see Fig. 3). Moreover, there was no difference in the proportion of grazing events on medusahead when lambs grazed with or without their mothers ($P > 0.05$).

Table 2
Proportion of grazing events recorded and the correlation coefficients *(r)* for those events between ewes and their respective lambs.

Grazing event[1]	Proportion (minimum-maximum)		*r*	*P* value
	Ewes	Lambs		
Supplemented sheep				
Total	0.40-0.74	0.36-0.97	0.58	0.0124
Medusahead	0.00-0.12	0.00-0.11	0.83	<0.0001
Other annual grasses	0.00-0.03	0.00-0.04	0.62	0.0059
Bunch grasses	0.23-0.50	0.26-0.67	0.52	0.0269
Forbs	0.07-0.28	0.06-0.25	0.33	0.1762
Nonsupplemented sheep				
Total	0.39-0.79	0.47-0.93	0.72	0.0008
Medusahead	0.01-0.12	0.00-0.10	0.83	<0.0001
Other annual grasses	0.00-0.02	0.00-0.03	0.24	0.3359
Bunch grasses	0.27-0.50	0.31-0.69	0.70	0.0013
Forbs	0.07-0.20	0.05-0.17	−0.08	0.7484

Eighteen ewes with their offspring were clustered into 6 groups, and they received an energy-rich supplement in the morning (supplemented ewes grazing with their offspring). A control group of 18 ewes clustered into 6 groups did not receive the supplement (nonsupplemented ewes grazing with their offspring).

[1] The proportion of grazing events was calculated from observations during 3.5 h of scan sampling (from 0830 to 1100 and from 1600 to 1700) during 6 d.

Table 3
Relative frequency and abundance and biomass (mean ± SEM) of medusahead and plant functional groups in plots grazed by ewes and their lambs.

	Medusahead	Plant functional groups: Other annual grasses	Bunch grasses	Forbs
Relative abundance on wet basis,[1] %				
Plots with supplemented sheep				
Pregrazing	5.8 ± 1.1	5.5 ± 0.4	25.7 ± 2.5	63.0 ± 3.8
Postgrazing	9.5 ± 4.8	3.4 ± 1.0	20.2 ± 1.9	66.9 ± 5.5
Plots with nonsupplemented sheep				
Pregrazing	2.7 ± 1.3	14.0 ± 3.2	27.3 ± 0.9	56.1 ± 3.6
Postgrazing	5.4 ± 3.9	5.7 ± 1.5	20.0 ± 2.0	68.8 ± 7.0
Harvested biomass by sheep,[2] kg dry matter plot^{-1} (0.09 ha)				
Sheep group				
Supplement	11.5 ± 5.4	21.6 ± 1.3	93.4 ± 6.2	120.3 ± 22.3
No supplement	3.5 ± 2.9	45.1 ± 10.4	72.3 ± 8.3	55.3 ± 13.2
Relative frequency,[1] %				
Plots with supplemented sheep				
Pregrazing	30.7 ± 4.8	49.3 ± 9.3	90.7 ± 1.3	100.0 ± 0.0
Postgrazing	48.0 ± 8.0	40.0 ± 0.0	66.7 ± 2.7	92.0 ± 0.0
Plots with nonsupplemented sheep				
Pregrazing	14.7 ± 5.8	69.3 ± 1.3	94.7 ± 1.3	98.7 ± 1.3
Postgrazing	22.7 ± 5.8	33.3 ± 5.8	72.0 ± 8.0	88.0 ± 2.3

[1] Visually estimated from 1 plot randomly selected from each of the 6 blocks present in the study; 3 plots were grazed by ewes with their lambs that received an energy supplement (supplemented sheep) and 3 plots were grazed by nonsupplemented ewes and their lambs (nonsupplemented sheep).

[2] Harvested biomass included biomass removed after grazing due to grazing or trampling.

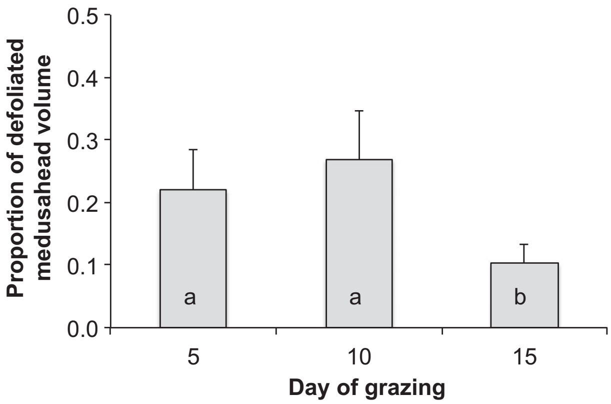

Figure 2. Average proportion of defoliated medusahead tillers by ewes and their lambs grazing medusahead-infested rangeland plots. The proportion of defoliated tillers in marked squares (90.2 cm^2) within each plot was estimated every 5 days. Vertical bars represent the standard errors of measurement. Days with the same letter did not differ ($P > 0.05$).

Evaluation of the Plant Community

The available biomass pregrazing was 34.6 kg DM $plot^{-1}$ (plot = 0.0105 ha). After grazing, the residual biomass was 2.1 kg DM $plot^{-1}$. The average relative abundance of plants (WB) for pregrazing was 19.9% ± 2.3% medusahead, 13.3% ± 1.5% other annual grasses, 36.1% ± 2.4% bunch grasses, and 30.8% ± 2.4% forbs. The average relative abundance of plants (WB) postgrazing was 37.1% ± 4.9% medusahead, 4.3% ± 0.7% other annual grasses, 23.0% ± 3.1% bunch grasses, and 35.5% ± 6.1% forbs.

Medusahead Defoliation

Weaned lambs with prior exposure to the supplement tended to defoliate a lower proportion of medusahead volume than nonsupplemented lambs ($P = 0.14$), 0.08 ± 0.03 versus 0.26 ± 0.09, respectively.

Average Daily Body Weight Change

Supplemented ewes lost 161.1 ± 106.7 g d^{-1} and nonsupplemented ewes lost 224.1 ± 124.4 g d^{-1} ($P = 0.95$). Likewise, supplemented lambs gained 150.2 ± 21.2 g d^{-1} and nonsupplemented lambs gained 117.8 ± 15.9 g d^{-1} ($P = 0.22$).

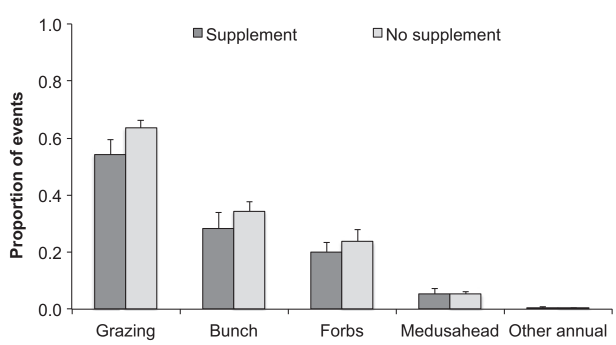

Figure 3. Daily average proportion of grazing events displayed by weaned lamb groups. Before weaning, six groups of lambs grazed with their mothers, but they received an energy-dense supplement before grazing their respective plots (Supplement); six other groups (No Supplement) did not receive the supplement. Grazing events were recorded using the scan sampling technique from 0830 to 1100 and from 1600 to 1700 when lambs grazed medusahead-infested rangeland plots. Vertical bars represent the standard errors of measurement.

Discussion

Medusahead and Ewe-Lamb Supplementation

A recent study suggests that energy-dense supplements increase the use of medusahead by lambs relative to nonsupplemented animals (Hamilton et al., 2015). Nevertheless, the increase reported in that study was modest and substantially below the intake capacity of the animals under study. A dietary ingredient, Ca-propionate, was added to the supplement used in the present study with the aim of further enhancing medusahead intake and animal performance relative to other supplements previously assayed. Propionate supplementation may improve ruminant nutrition when glucogenic precursors are inadequate due to low-quality diets and/or increased energy demands (Mulliniks et al., 2011). Despite this addition, the supplement used in this study did not have an effect on medusahead use. Consistent with these results and under more controlled experimental conditions in pens, Villalba and Burritt (2015) did not find a positive effect of energy supplements containing Ca-propionate on intake of medusahead by lambs.

A lower number of grazing events was recorded for medusahead than for bunch grasses, even when medusahead showed a greater content of CP and lower concentration of fiber than did bunch grasses. However, medusahead had 61% more AIA (approximation of silica content) than bunch grasses at the beginning of the study. Silica decreases preference for grasses in rabbits (Cotterill et al., 2007), voles (Massey and Hartley, 2006), and sheep (Massey et al., 2009) when its concentration increases in the plants' tissues, according to species, maturity stage, and anatomy part. Amorphous silica is a structural component of the grass epidermis, representing a physical barrier (Mayland and Shewmaker, 2001) against breakup of plant tissues and thus a restriction for the release of nutrients to the rumen environment (Bae et al., 1997; Hunt et al., 2008). This constraint decreases the rate of fermentation, as in vitro digestibility studies have shown (Montes, 2016). Thus, it is likely that due to this blocking action of silica on forage digestion, the influence of supplements at enhancing use of medusahead by ruminants is attenuated or prevented as observed in this and previous studies (Hamilton et al., 2015; Villalba and Burritt, 2015).

Use of Medusahead Relative to Its Abundance

Ewes and their lambs grazing together and lambs grazing alone displayed low levels of medusahead use during grazing, ~5% of grazing activities. Consistent with this finding, Yiakoulaki et al. (2009) reported that *T. caput-medusae* (unknown subsp.) represented 6.4% of the diet in adult ewes grazing in the natural habitat of this grass (i.e., Greece).

The estimation of biomass harvested by sheep in this study showed that medusahead represented approximately 3% of the ewes and lambs' diet, below the 5% average recorded during scan sampling. The former may represent an underestimation as medusahead might have increased in frequency during the grazing period (2 − 16 June 2013), a pattern that was observed in June 2014 (Montes, 2016). This increase in medusahead frequency during grazing may be attributed to the fact that medusahead grows 2 weeks later than native plants (Young, 1992).

Collectively, our results suggest that when the relative abundance of medusahead in a plant community is below a certain threshold (i.e., 6% in plots grazed by ewes and their lambs), animals may not avoid this weed despite its low palatability. In contrast, when sheep are exposed to ad libitum amounts of medusahead and then to a basal diet of grass hay, the proportion of medusahead in the diet declines drastically, indicating in these conditions a clear state of avoidance (Hamilton et al., 2015; Villalba and Burritt, 2015). Such avoidance was also observed in the weaned lambs, which grazed plots with a greater degree of medusahead infestation (i.e., 20% relative abundance).

Herbivores exposed too frequently or to too much of a specific feed will satiate on that feed, decreasing their preference relative to an alternative feed (Provenza, 1996). Satiation may create mild to strong states of feed aversion that are more pronounced when feeds are nutritionally imbalanced or when they contain toxins (Provenza, 1996). Medusahead ingestion could lead to nutrient imbalances as its digestion is impaired by the antinutritional factor silica as described earlier, which may induce a strong state of avoidance when exposure to the weed is high (i.e., herbivores grazing medusahead monocultures). In contrast, when the abundance of medusahead is low, the negative postingestive consequences of the weed (e.g., poor digestibility, low release of nutrients) may be diluted and thus experienced to a lesser extent by the herbivore. In addition, the ingestion of additional nutritious plants from the community may attenuate the typical aversive responses to medusahead observed when the weed is abundant. It is likely that the diversity of plants available in the plots of this study provided the appropriate nutritional context to at least prevent the avoidance of the weed, an effect that in turn reduced the potential positive impact of the supplement on medusahead use by ewes and their lambs.

Use of Medusahead Across Days

Ewes and their lambs displayed more foraging events on medusahead toward the second half of the grazing period, even when medusahead was at mid to late reproductive stage with lower CP content and greater AIA content than when the weed was less mature—at the beginning of the grazing period. This foraging pattern could be explained by the fact that animals became more familiar with the weed because familiarity with a certain feed increases preference (Provenza, 1995). Alternatively, the presence of inflorescences in more mature plants may have contributed to an increased intake as sheep show greater preferences for medusahead inflorescences than for leaves and stems (Villalba and Burritt, 2015). Preference for medusahead inflorescences could be due to the greater DM digestibility (68.0%) and the lower concentration of AIA (7.7%) for this plant component than for stems and leaves (57.8% of DM digestibility and 9.3% of AIA) (Montes, 2016).

Despite the greater use of medusahead toward the end of the grazing trial revealed during scan sampling, this pattern was not reflected in the proportion of defoliated medusahead volume recorded in the vegetation during that period (i.e., from day 10 to day 15). It is possible that the depletion of biomass (and thus inflorescences) in the small squares attenuated the effect observed at a larger scale with more ungrazed plants available during scan sampling.

Effects of Experience on Medusahead Use by Weaned Lambs

Weaned lambs had experience at grazing medusahead with their mothers, and such experience likely allowed them to include a greater proportion of medusahead into their diet after weaning. Ramos and Tennessen (1992) reported that experience with mothers increases the initial acceptance of pasture and preference for specific forages. The sensitive period for young herbivores to learn from their mothers is during the transition from monogastric to ruminant digestive physiology—weaning (Provenza and Balph, 1987).

Individual Variation in the Use of Medusahead

Animal-to-animal variability is common within species, breeds, and even for a given herd or flock regarding the propensity to consume certain plants in a community such as woody species (Baraza et al., 2009; Estell et al., 2012). Consistent with this variability, sheep show individual variation with regard to the amount of medusahead they can ingest. For instance, ewes and their lambs showed variation in the proportion of grazing events recorded for medusahead (i.e., 0% to 12%) in this study. Similarly, Hamilton et al. (2015) and Villalba and Burritt (2015) found clear individual variation with regard to medusahead intake by lambs 2 − 3 months of age.

The relative extent of medusahead use by mothers (low, medium, or high) was reflected in the use of medusahead by their offspring. Thus, results from this study suggest that individual variation in medusahead use is passed from mother to offspring, through genetics and/or observational learning. Social models play a key role in diet selection and food preferences of young ruminants (Thorhallsdottir et al., 1987). As offspring begin to forage, they further learn what to eat (e.g., Mirza and Provenza, 1990, 1992; Thorhallsdottir et al., 1990) and where to go (i.e., Howery et al., 1998) from their mothers. It may be possible to capitalize on this individual variation for targeted grazing treatments by selecting females, through either genetic markers or observation, that show a high propensity to consume medusahead as they most likely will have offspring with similar dietary habits.

Animal Performance

Supplementation had no effect on animals' performance; ewes lost similar weight and lambs gained similar weight during grazing. Moore et al. (1999) reported that supplementation does not ensure weight gain in cattle, and in many cases, weight does not increase when forages are supplemented and sometimes even decreases. Similarly, Caton and Dhuyvetter (1997) found that the majority of data about energy supplementation at pasture suggests that it does not influence production or that it reduces weight and body condition score in cows. The variation in the effect of energy supplementation depends on the chemical characteristics of supplements and forages, amounts, and increments in animal's maintenance needs under grazing.

Implications

Sheep ate low amounts of the unpalatable weed medusahead, and an energy-based supplement did not affect this outcome. Nevertheless, despite its low palatability, sheep did not select against medusahead when grazing moderately infested rangeland, a foraging pattern that does not confer a competitive advantage to the weed. Thus, managing grazing in moderately infested pastures without supplementation may prevent spread of the weed. Weaned lambs may continue harvesting medusahead at similar proportions to those observed before weaning, without the need to learn from trial and error, thus reducing the period of time needed to ingest medusahead to their capacity. A delay in animals learning to ingest medusahead due to unfamiliarity will make the weed more unpalatable due to maturity and increase the likelihood of dropping viable seeds into the soil. Finally, it may be possible to select reproductive females with greater preference for medusahead and establish homogeneous flocks with greater capacity to harvest medusahead.

Acknowledgments

This paper is published with the approval of the Director, Utah Agricultural Experiment Station, and Utah State University, as journal paper number 8891. We acknowledge T. Lisonbee, T. Grisenti, G. Johnson, T. Hamilton, C. Spackman, and K. Price for technical support; A. Boca for soil analyses; and K. Bear and J. Pfister for laboratory space.

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