Effects of early experience and alternative feeds on medusahead (*Taeniatherum caput-medusae* ssp. *asperum*) intake by sheep

Juan J. Montes-Sánchez^{a,1} and Juan J. Villalba^a

^aWildland Resources, Utah State University, Logan, Utah, 84322, USA

E-mails: montesjujo@yahoo.com.mx; juan.villalba@usu.edu

Corresponding author:

Juan J. Montes-Sánchez

E-mail: montesjujo@yahoo.com.mx

¹ Present address: Centro de Investigaciones Biológicas del Noroeste Unidad Guerrero Negro, Programa de Agricultura en Zonas Áridas, Guerrero Negro, Baja California Sur, Mexico, 23940.

Abstract

The goals of this study were to test the effects of early experience at grazing medusahead –an invasive unpalatable weed - and the availability of forage alternatives on intake of medusahead later in life by sheep. The study involved two experiments of 10 days each. During Experiment 1, 29 yearling sheep were penned individually in a 2x2 factorial design with early experience at grazing medusahead (yes [$n = 15$], no [$n = 14$]) and alfalfa hay availability (yes, no) as the main factors. All animals were fed *ad libitum* amounts of freshly harvested medusahead daily from 10:00 to 13:00 h; additionally, eight experienced and seven inexperienced sheep received alfalfa hay (0.31% body weight) at the same time. All groups had a basal diet of tall fescue hay. Intake of the forages, NaCl and trace-mineralized salt blocks was measured. In Experiment 2, sheep were then clustered into nine groups of three yearlings each ($n = 5$ early experience; $n = 4$ experience gained during Experiment 1) and one group of two yearlings (experience gained during Experiment 1) and grazed 10 plots of medusahead-infested rangeland. Grazing events were recorded daily at 5 min intervals from 08:30 to 11:00 h and from 16:00 to 17:00 h, and the defoliation proportion of medusahead tillers was determined every five days. During Experiment 1, medusahead intake was not affected by early experience or alfalfa availability ($P > 0.05$) but medusahead intake across days was cyclic with more pronounced intake peaks at the beginning and end of the experiment for inexperienced animals ($P < 0.05$). Experienced sheep showed a greater gain-to-feed ratio ($P < 0.05$), and tended to have greater average daily body weight gains and salt intake ($P < 0.10$) than inexperienced sheep. Sheep fed alfalfa tended to eat less trace-mineralized salt blocks than sheep that did not receive this forage ($P < 0.10$). During Experiment 2, the proportion of grazing events recorded on medusahead by both groups (yes/no early experience) of animals was almost nil, although experienced animals tended to defoliate more medusahead tillers than inexperienced animals ($P = 0.10$). In conclusion, when sheep were fed *ad libitum* amounts of medusahead, intake was low and cyclic with a more even consumption of the weed by experienced animals. Under these conditions, early experience also

51 favored animal performance. However, it is likely that such high exposure to medusahead
52 attenuated the subsequent use of the weed during grazing.

53
54 **Keywords:** grazing, diet selection, feed preference, weed control

56 1. Introduction

57 Medusahead (*Taeniatherum caput-medusae* ssp. *asperum*) is a Eurasian annual grass
58 that due to its invasiveness and poor nutritional quality negatively impacts the structure and
59 functioning of rangeland ecosystems (Young, 1992; Davies and Johnson, 2008). The spread of
60 this weed threatens millions of hectares of rangeland in the western United States despite the
61 different methods attempted for its control (Sheley and James, 2010; Davies and Sheley, 2011).
62 Grazing represents a sustainable and successful alternative for the control of invasive plant
63 species (Frost and Launchbaugh, 2003; Vavra *et al.*, 2007), which is typically conducted with
64 domestic sheep and goats. Nevertheless, results regarding the control of medusahead through
65 grazing have been poor and variable (James *et al.*, 2015), an outcome attributed to the low
66 intake and palatability of this weed (Young, 1992). Despite this constraint, stakeholders involved
67 in the medusahead management in the United States list grazing as a preferred management
68 tool to control medusahead (James *et al.*, 2015).

69 Foraging decisions by herbivores can be modified by environmental experiences
70 (Provenza and Balph, 1987), which in turn influence animal fitness and in the process, the
71 structure and composition of plant communities (Provenza and Balph, 1990). In this regard, the
72 mother represents a key social model, which allows the offspring to better adapt to novel foods
73 and habitats (Provenza and Balph, 1987). For instance, the mother increases the efficiency of
74 learning about novel nutritious foods and reduces the risk of overingesting poisonous plants
75 (Provenza, 1996). Young animals learn with their mothers to consume low-quality forages (Distel
76 *et al.*, 1994), as early experiences have life-long influences on herbivores by causing

neurological, morphological, and physiological changes (Provenza and Balph, 1990) through changes in gene expression (Fish *et al.*, 2004) which allow for a greater efficiency of nutrient use (Distel *et al.*, 1994; Chadwick *et al.*, 2009).

In addition to the influence of the mother, individual experiences with the chemical and physical characteristics of the feed environment have significant impacts on herbivores' foraging decisions (Provenza, 1996; Provenza and Villalba, 2006). For instance, intake of and preference for an unpalatable food can increase when its ingestion is associated with the consumption of a high-quality supplement in a sequence familiar to the animal (Provenza *et al.*, 2003; Baraza *et al.*, 2005). Certain nutrients in the associated plant community or provided by supplements (i.e., carbohydrates and proteins, minerals) have the potential to increase preference for poor-quality forages (Provenza *et al.*, 2003). Thus, experiences early in life with the mother and an additional availability of nutrients may act synergistically to enhance use of unpalatable forages like medusahead by herbivores, an effect which may persist throughout the life of an individual and across generations. In turn, these responses will contribute to a more even utilization of resources in a plant community (e.g., palatable and unpalatable plants) and as a consequence, to the maintenance of biodiversity in the landscape (Provenza *et al.*, 2003).

We hypothesized that yearling sheep will increase their utilization of medusahead when they are exposed to medusahead with their mothers early in life and when supplemental feeds are available. To test this hypothesis we determined the effects of early experience at grazing medusahead and the availability of additional feeds (alfalfa hay, forages provided by the plant community) on intake of medusahead by sheep fed in confinement and during grazing.

2. Materials and Methods

2.1. Exposure to Medusahead

Thirty-six crossbred ewes with their lambs (2-3 months old) grazed medusahead-infested rangeland with a moderate (~10% in the plant community) level of medusahead infestation during June of 2013. Details for this exposure are presented in Montes (2016). Briefly, the

foraging behavior of ewes and their lambs grazing medusahead-infested rangeland was recorded at 5-min intervals from 08:30 to 11:00 h and from 16:00 to 17:00 h for 12 days using the scan sampling technique (Altman, 1974). The average percentage of events recorded for lambs eating medusahead was $4.4 \pm 0.5\%$ of the total observed behavioral events and $58.0 \pm 3.3\%$ of the total observed behavioral events involved grazing activities.

After exposure to medusahead, 15 randomly-selected lambs (experienced animals) out of a group of 49 were kept in an orchardgrass (*Dactylis glomerata*) pasture from June 24 of 2013 to May 5 of 2014 and fed alfalfa (*Medicago sativa*) hay in *ad libitum* amounts from November 2013 to March 2014. Animals then received a diet of endophyte-free tall fescue (*Festuca arundinacea*) hay from April 1 to May 5 of 2014. Additionally, 15 lambs of similar age (8 months old) without exposure to medusahead (inexperienced animals- Controls) were kept in the same orchardgrass pasture from October 20, 2013 to May 5, 2014 and received the same feeding regime described for experienced lambs. During summer of 2013, and prior to joining the experienced group of lambs, inexperienced lambs consumed high-quality feedstuffs in pens from May to July 2013 (i.e., alfalfa pellets, barley grain, and beet pulp) and from August to October 2013 they grazed irrigated high-quality pastures (tall fescue, sainfoin [*Onobrychis viciifolia*] and alfalfa).

2.2. Experiment 1. Experience early in life and availability of alfalfa hay

All animals were kept outdoors at the Green Canyon Ecology Center located in Logan, UT, USA. On May 6, 2014, all yearling sheep were individually penned outdoors, under a protective roof in individual, adjacent pens measuring 1.5 × 2.5 m; alfalfa pellets were used as the basal diet until a day previous to harvested medusahead exposure (May 27). A period of adaptation to medusahead was not carried out because medusahead is an annual grass with a very short growth period. For instance, medusahead matured from the late vegetative to the late reproductive phenological stage in 17 days during June of 2013 (Montes, 2016). Animals had free access to fresh water, salt and trace-mineralized salt blocks throughout the study. Research

protocols were conducted according to procedures approved by the Utah State University Institutional Animal Care and Use Committee (Approval # 1551).

Experienced and inexperienced yearlings with an average body weight (BW) of 58.7 ± 5.7 kg were blocked by BW and randomly assigned to one of four treatments: experience with medusahead + alfalfa hay ($n = 8$), experience with medusahead without alfalfa hay ($n = 7$), inexperience with medusahead + alfalfa hay ($n = 7$), and inexperience with medusahead without alfalfa hay ($n = 7$). One inexperienced animal died in the fall of 2013 and as a consequence each inexperienced group had 7 animals.

Alfalfa and endophyte-free tall fescue hays were passed through a hydraulic bale grinder (Gehl commercial forage grinder) and chopped into particles of 4-6 cm length.

A naturally established stand of medusahead growing in private land within the city limits of Paradise, Cache County, UT ($41^{\circ}34'03''\text{N}$ and $111^{\circ}50'02''\text{W}$) was harvested daily using a lawnmower (particle size 4-5-cm length) during the reproductive stage, transported to the Green Canyon Ecology Center, homogenized and fed to all yearlings on a daily basis.

Chopped alfalfa hay and chopped fresh medusahead were presented in two different feeders in each individual pen at 10:00 h. The amount of chopped alfalfa hay was restricted to 187.5 ± 19.5 g of dry matter (DM) per day (0.31% of initial BW) and it was consumed in less than 20 min. Thus, the empty feeders that contained alfalfa hay were removed daily from all pens at 10:20 h. Medusahead refusals were removed at 13:00 h and intake was calculated by subtracting the amount of feed refused from the amount of feed offered. All animals were then offered chopped endophyte-free tall fescue hay in *ad libitum* amounts from 13:00 to 15:00 h. At 15:00 h, refusals were collected and no other feed was offered until the next day. Tall fescue hay intake was estimated as described before. The experiment was conducted for 10 days, from May 28 to June 6, 2014.

Intake of salt blocks (NaCl [98.0-99.9%]; White Salt Block, North American Salt Company, Overland Park, Kansas, USA) and trace-mineralized salt blocks present in each pen

(NaCl [93-98%], Zn [$\geq$ 3500 ppm], Mn [$\geq$ 2800 ppm], Fe [1750 ppm], Cu [350-450 ppm], I [70 ppm], Co [70 ppm]; Morton iOfixt T-M, Chicago, IL, USA) were determined by subtracting the initial weight from the current weight of the block on days 2, 4, 6, 8, and 10 of the experiment. Salt and trace-mineralized salt block weights were determined at the same time (from 10:00 to 11:00 h) during those days.

Samples of offered and refused forages and salt blocks were dried in an air forced oven at 60°C for 48 h to report intake values on DM basis. Samples of offered forages were then ground using a Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA) with a 1-mm screen for chemical analyses. Yearlings were weighed at the end of the experiment and average daily BW gain and gain-to-feed ratio (kg of BW gain:kg of DM intake) were calculated.

2.3. Experiment 2. Effect of experience on grazing medusahead-infested rangeland

2.3.1. Study area

All yearlings from Experiment 1 were transported to privately-owned land in Mantua, UT, USA (41° 29'51" N and 111°56'32" W). The ecological site is a Mountain Stony Loam, where the plant community is Mountain Big Sagebrush with introduced non-native species (Wadman, 2012); the study area had a moderate level of medusahead infestation (for more detail see Section 3.2. 1.). Five blocks (0.18 ha/block), each divided into two plots (0.09 ha/plot) were marked on this area. Each plot was delimited using electric fence and a pen of ~3.0 m² was assembled outside each plot for overnight enclosure of the animals. Three control plots (no grazing) were located between the grazed blocks.

2.3.2. Experimental Protocol

All yearling sheep had experience with ingesting medusahead after Experiment 1. However, just one group of 15 yearling sheep had experience early in life with grazing medusahead-infested rangeland. Sheep were randomly clustered into 10 groups of three yearlings each with the constraint that animals with and without experience early in life with grazing medusahead were kept in separate groups ($n = 5$ groups formed with yearlings with

experience early in life with grazing medusahead; $n = 5$ groups formed with yearlings with experience gained during Experiment 1). One group with experience gained during Experiment 1 had two yearlings, as one animal was lost in the fall of 2013. Groups were randomly assigned to the plots within each block with the constraint that an experienced and an inexperienced group grazed within each block. The experiment was conducted for 10 days (June 10 to 19) during the reproductive stage of medusahead. Animals had free access to water, salt and trace-mineralized salt blocks throughout the experiment.

Animals grazed from 08:30 to 17:00 h and they were then penned overnight. The behavioral activity of yearlings was recorded at 5-min intervals from 08:30 to 11:00 h and from 16:00 to 17:00 h using the scan sampling technique (Altman, 1974). Four observers recorded the animals' foraging activities by direct observation within a distance of ≈ 1 -3 m from the yearlings since all animals were accustomed to the observers' presence. Two observers scanned yearlings from two continuous plots and the other two observers scanned yearlings from three continuous plots. Additionally, observers rotated across plots throughout days during morning and evening scans. Foraging activities involved those events when animals were observed grazing medusahead, annual grasses other than medusahead, bunch grasses, and forbs in the plant community; other activities were: walking, resting, ruminating, and drinking. The proportion of grazing events on medusahead and other functional groups in the community relative to the total number of scans recorded was determined daily. Animals were weighed at the end of the grazing trial to calculate the average daily BW change.

2.3.3. Evaluation of the plant community

Plant biomass production was estimated using a rising plate meter (Michell, 1982). Twenty-five readings of plant height were recorded along a zig-zag transect per plot pre- and post-grazing using the rising plate meter (plate area = 0.0985 m^2). Plant DM in each plot for calibration curves was assessed pre- and post-grazing by taking 27 random readings of the rising plate meter (Michell, 1982) during each period along with DM production values.

The relative fresh biomass abundance pre- and post-grazing of medusahead and different plant functional groups (forbs, bunch grasses, and annual grasses other than medusahead) were visually estimated in 25 squares ($0.0985 \text{ m}^2/\text{square}$), randomly distributed within a zig-zag transect per plot.

Four squares ($0.0985 \text{ m}^2/\text{square}$) 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. A composite of medusahead and functional groups was formed with samples from three plots. Samples were dried in a forced air oven at 60°C until constant weight and ground using a Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA) with a 1-mm screen for chemical analyses.

2.3.4. Medusahead defoliation

Ten squares (0.009 m^2) with medusahead tillers were marked on the soil of each plot; the squares were made with flagging tape, which was anchored to the soil with nails at each square corner; this was a modification for marking bunch grasses as described by O'Reagain and Grau (1995). A numbered flag was inserted into the soil about 40 cm from each square to target the area and reduce possible cueing effects on grazing behavior. Medusahead cover into each square was ranked from 1 to 5 according to the proportion of soil occupied by medusahead tillers: 1 = 10% cover (0.0009 m^2), 2 = 30% cover (0.0027 m^2), 3 = 50% cover (0.0045 m^2), 4 = 70% cover (0.0063 m^2), and 5 = 90% cover (0.0081 m^2). Medusahead tillers within each square had similar height and the length of the tallest leaf in the tillers was measured. The estimated area of tillers multiplied by the height of the tallest leaf was used to estimate the initial volume of the biomass contained into the marked square immediately before grazing. On days 5 and 10 and after scan sampling, the proportion of defoliated tillers was visually estimated (defoliated area) and multiplied by the height of the tallest leaf remaining on the tillers to estimate the volume of biomass after grazing. The proportion of medusahead volume removed (MR) during grazing was calculated as:

$$MR = \frac{\text{Initial volume (m}^3\text{)} - \text{Volume after grazing (m}^3\text{)}}{\text{Initial volume (m}^3\text{)}}$$

(1)

2.4. Chemical analyses

Ground samples from Experiment 1 (medusahead collected on days 1 [May 28], 4 [May 31], 7 [June 3], and 10 [June 6], and alfalfa and tall fescue hays) and Experiment 2 (3 spatial replicates of medusahead, other annual grasses, bunch grasses, and forbs before and after grazing) 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 concentration by 6.25. NDF and ADF contents were measured according to Van Soest et al. (1991), ADF determination was sequential of NDF, and heat stable amylase was used to measure NDF. Ash content was obtained by burning samples at 550°C for 6 h (Allen, 1989). Acid insoluble ash is an estimate of silica content (i.e., > 90% of AIA is silica [Charca et al., 2007]) and it was determined by the method of 2N HCl (Van Keulen and Young, 1977).

2.5. Statistical analyses

Analyses were computed using SAS (SAS Inst., Inc. Cary, NC; Version 9.1 for Windows). The covariance matrix structure used was the one that yielded the lowest Akaike information criterion (i.e., first-order autoregressive). The assumptions of normal distribution and homocedasticity were examined by plotting residuals vs. predicted value and quantile. Data were transformed according to the Box-Cox method. Medusahead intake was square transformed, intake of salt blocks were $\ln(x + 1)$ transformed, and proportions of scan sampling and medusahead defoliation were arcsine-squareroot transformed to meet the test assumptions. Non-transformed means $\pm$ standard error of the mean (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 $0.05 < P < 0.15$. One outlier (an inexperienced animal that did not receive alfalfa hay during Experiment 1) was removed from all analyses.

Feed intake, average daily BW gain, and gain-to-feed ratio in Experiment 1 were analyzed as a mixed model in a 2x2 factorial design with early experience (yes, no) and availability of alfalfa hay (yes, no) as the main factors with sheep (random effect) nested within treatment group (experience and availability of alfalfa as fixed effects), and day (feed intake and scan-sampling data) as the repeated measures.

The proportion of events for grazing medusahead, annual grasses, bunch grasses, and forbs, and percentage of medusahead volume removed during grazing in Experiment 2 were analyzed as a mixed-model effects with block as a random effect and experience and day as fixed effects. Average daily BW gain per group was analyzed using a one-way analysis of covariance with experience as a fixed factor and the average initial BW per group as a covariate.

The content of CP, NDF, ADF, ash, and AIA was compared using a two-way analysis of variance with functional group, time of sampling (pre- and post-grazing) and their interaction as the main factors.

3. Results

3.1. Experiment 1. Experience early in life and availability of alfalfa hay

3.1.1. Chemical composition of the forages

Chemical composition of offered forages is shown in Table 1. Medusahead showed the lowest content of CP and the greatest contents of ash and AIA, which remained fairly constant throughout the study.

3.1.2. Intake of tall fescue hay

The individual average intake of tall fescue increased every day until day 5 ($P < 0.0001$); intakes on days 1 to 4 were 590.0 ± 30.5 g, 649.3 ± 30.9 g, 847.8 ± 29.5 g, and 951.3 ± 25.9 g, respectively, and the average intake after day 5 was 1038.8 ± 31.8 g/day/yearling.

3.1.3. Intake of medusahead

No difference in medusahead intake was detected between groups of yearlings with or without early experience with grazing medusahead ($P = 0.48$); average daily DM intake by experienced and inexperienced sheep was 41.8 ± 7.0 g and 37.6 ± 8.9 g, respectively. Availability of alfalfa hay did not favor intake of medusahead ($P = 0.45$); average daily DM intake by sheep with and without alfalfa hay was 38.2 ± 8.1 g and 37.0 ± 5.8 g, respectively. Likewise, alfalfa hay availability did not influence intake of medusahead by either the experienced or inexperienced group of animals (experience $\times$ alfalfa availability effect; $P = 0.24$); average daily DM intakes were: experience with medusahead + alfalfa hay, 46.1 ± 8.2 g; experience with medusahead without alfalfa hay, 33.5 ± 5.6 g; inexperience with medusahead + alfalfa hay, 34.6 ± 10.5 g; inexperience with medusahead without alfalfa hay, 41.0 ± 7.6 g.

Sheep consumed different amounts of medusahead across days ($P < 0.0001$; Fig. 1A), yearling sheep showed a cyclic pattern of medusahead intake, with peaks of greater intake during days 1 and 10, and a subtle intake peak on day 6.

Experienced and inexperienced sheep showed different intakes of medusahead across days (experience $\times$ day; $P = 0.04$; Fig. 1B). Inexperienced sheep had a well-defined intake peak during the first day of medusahead exposure, followed by lower intake values during 7 days and a subsequent increment on days 9 and 10. Daily intake of medusahead by experienced animals was more even than for inexperienced animals, as medusahead consumption by the experienced group did not differ across days. Moreover, intake of medusahead by experienced animals on days 1, 5, 6, 7, 9, and 10 was not different from the greatest peak displayed by inexperienced animals during day 1.

3.1.4. Intake of salt blocks

Sheep ate different amounts of salt across days ($P = 0.0004$; Fig. 2). Sheep ate more salt on day 10 than on day 8. Averaged across days, experienced animals tended to eat more salt than inexperienced animals (11.8 ± 3.9 vs. 5.4 ± 2.0 g, respectively, $P = 0.09$), and experienced sheep tended to eat more salt than inexperienced sheep when both groups did not receive

alfalfa (12.8 ± 5.1 vs. 2.5 ± 1.0 g, respectively; $P = 0.13$). Sheep reduced intake of trace-mineralized salt across days ($P < 0.0001$; Fig. 2). Animals without alfalfa hay tended to eat more trace-mineralized salt blocks every 2 days than animals that received this forage (12.2 ± 4.0 vs. 6.9 ± 2.2 g, respectively; $P = 0.09$).

3.1.5. Average daily body weight gain and gain-to-feed-ratio

Average daily BW gain tended to be greater for experienced than for inexperienced animals (306.2 ± 44.6 vs. 191.8 ± 27.2 g/day, respectively; $P = 0.07$). Experienced animals showed a greater gain-to-feed ratio than inexperienced animals (0.29 ± 0.05 vs. 0.20 ± 0.01 kg of BW gain/kg DM intake; $P = 0.03$).

3.2. Experiment 2. Effect of experience on grazing medusahead-infested rangeland

3.2.1. Plant community

Biomass availability in grazed plots pre- and post-grazing was 351 ± 18 and 247 ± 18 kg DM, respectively. During the same period, the biomass available in the ungrazed plots increased from 358.3 ± 20 to 531 ± 64 kg DM. The relative fresh biomass abundance of plant groups pre- (grazed and ungrazed plots) and post-grazing (grazed plots) were, respectively: $6.3 \pm 1.5\%$ and $9.5 \pm 1.5\%$ medusahead, $6.3 \pm 2.0\%$ and $3.9 \pm 1.3\%$ annual grasses other than medusahead, $30.1 \pm 2.8\%$ and $34.5 \pm 3.5\%$ bunch grasses, and $57.3 \pm 3.4\%$ and $52.1 \pm 3.5\%$ forbs. Whilst in ungrazed plots the relative fresh biomass abundance after grazing period were $10.3 \pm 0.3\%$ medusahead, $11.5 \pm 2.7\%$ annual grasses other than medusahead, $21.8 \pm 2.4\%$ bunch grasses, and $56.4 \pm 1.4\%$ forbs.

3.2.2. Chemical composition of plants

The chemical composition of the plant community where yearlings grazed is shown in Table 2. Different functional groups had different content of CP, NDF, ADF, ash, and AIA (Table 2). Forbs and medusahead had the greatest content of CP and bunch grasses had the lowest content of CP. Bunch grasses had the greatest content of NDF and ADF, and forbs showed the lowest concentration of these plant cell wall fractions. Medusahead had the greatest content of

ash and AIA; forbs had an intermediate content of ash but the lowest content of AIA, whereas annual and bunch grasses had the lowest content of ash, and intermediate content of AIA.

Before grazing, plants had greater content of CP and ash, lower content of NDF and ADF (Table 2), and tended to have lower AIA ($P = 0.11$). There was interaction between group of plant and sampling date noting the increment of ADF as mature bunch grasses and annual grasses other than medusahead (Table 2).

3.2.3. *Use of the plant community*

Sheep showed different proportion of grazing events during different days of the experiment (Fig. 3). Sheep increased the proportion of grazing events on day 3, increased again on day 7, and then they gradually declined. Early experience with grazing medusahead-infested rangeland did not have an effect on the proportion of total grazing events recorded ($P > 0.05$).

The proportion of events recorded for eating forbs decreased across days, whilst a contrasting pattern was observed for scans recorded for ingestion of bunch grasses (Fig. 3). Early experience with grazing medusahead-infested rangeland or its interaction with day did not have an effect on the proportion of events recorded for grazing forbs and bunch grasses ($P > 0.05$).

The proportion of events recorded for grazing annual grasses was not affected by early experience with grazing medusahead-infested rangeland, day, or their interaction (Fig. 3). The use of medusahead by sheep was almost nil; the proportion of grazing events on medusahead was 0.0044 ± 0.0000 , with no effect of any factor ($P > 0.05$).

3.2.4. *Medusahead defoliation*

Animals with experience early in life at grazing medusahead tended to defoliate more volume of medusahead tillers than the inexperienced animals ($P = 0.10$), as the average proportion of defoliated volume every 5 days was 0.022 ± 0.011 for experienced animals and 0.006 ± 0.000 for inexperienced animals. Day or its interaction with experience early in life at

grazing medusahead did not have an effect on the proportion of defoliated volume of medusahead tillers ($P > 0.05$).

3.2.5. Average daily body weight change

Yearlings lost weight during the grazing trial, but there were no differences in the daily loss between experienced and inexperienced groups ($P = 0.75$), 353.9 ± 68.2 g/day and 338.5 ± 46.7 g/day, respectively. The average body weight of all animals after grazing was $57.0 \text{ kg} \pm 1.0$ kg.

4. Discussion

4.1. Cyclic pattern of medusahead intake

Intake of medusahead by yearling sheep was low and cyclic, which is consistent with previous research conducted in lambs (Hamilton et al., 2015; Villalba and Burritt, 2015). Feed intake across days by herbivores becomes cyclic when animals eat a certain food and then they experience negative post-ingestive consequences due to an excess of nutrients released into the gastrointestinal tract from rapidly fermentable foods, due to nutrient deficiencies or due to toxins (Provenza, 1996). Medusahead is not toxic (Hamilton et al., 2015) or rich in nutrients but high in the concentration of the anti-nutritional component silica, as shown in this study by the high content of AIA recorded for this weed. Silica is involved in the reduction of preference for grasses by herbivores and this effect is more pronounced as its content in plant tissues increases (Massey et al., 2009). The effect of this anti-nutritional factor may contribute to the cyclic pattern of medusahead intake.

The interaction between the sensorial characteristics of feeds (sensory-specific responses) and their post-ingestive effects (nutrient-specific responses) affect preference, being difficult to isolate the independent effects of either (Provenza and Villalba, 2006). Animals decrease feed intake when they only receive chemo-sensorial stimulation or chemo-sensorial stimulation matched with intragastric infusions of non-nutritive solutions (Rolls, 1986). This response may be due to the lack of positive post-ingestive feedback that typically stimulates

385 feeding (Provenza, 1996). The silicified epidermis in grasses represents a physical barrier
386 (Mayland and Shewmaker, 2001) that decreases the breakup of forages and release of nutrients
387 (Bae et al., 1997; Hunt et al., 2008), which decreases the rate of fermentation as observed for
388 medusahead (i.e., Montes, 2016). Thus, the slow availability of nutrients from medusahead may
389 produce weak positive post-ingestive feedback signals that do not encourage further
390 consumption or preference for this weed.

391 Peaks and nadirs of medusahead intake were more evident for inexperienced animals,
392 whereas intake was more even for experienced yearlings. The slow breakup and fermentation of
393 medusahead could increase fill effects in the rumen and reduce passage rate through the
394 reticulorumen (Montes, 2016). Considering that positive experiences early in life can have life-
395 long influences on herbivores by causing neurological, morphological, and physiological
396 changes (Provenza and Balph, 1990), experienced yearling could have had a greater number of
397 rumination events - the major force in reducing particle size (Van Soest, 1994) - thus reducing fill
398 effects and increasing the passage rate of medusahead. This effect was likely enough to change
399 the feeding pattern but not high enough to promote greater differences in daily feed intake.

400 The availability of alfalfa hay did not change the nutritional context to favor an increment
401 in medusahead intake by sheep. It is worth mentioning that alfalfa is a legume of high protein
402 content (NRC, 2007) and Hamilton et al. (2015) reported that lambs tended to eat more
403 medusahead when they were supplemented with a high-energy concentrate. Nevertheless, the
404 presence of alternative high-quality foods does not typically lead to clear increments in
405 medusahead intake by sheep (Hamilton et al., 2015; Villalba and Burritt, 2015) likely due to the
406 aforementioned digestibility constraints imposed by silica (Montes, 2016).

407 In addition to cyclic patterns of intake, there is a great deal of variation in medusahead
408 intake among individuals. This variability was also observed during this study in yearlings with
409 and without experience, and in lambs with different types of supplement (energy and protein

concentrates; Hamilton et al., 2015), or energy concentrates containing different feed additives (Ca-propionate or yeast culture; Villalba and Burritt, 2015).

4.2. Salt intake

Grasses are relatively rich in minerals, with low contents of sodium and high concentrations of potassium (Bell, 1972). Sodium content in plants varies seasonally and many grazers, including sheep, may become sodium deficient (NRC, 2007). Experienced yearlings likely learned to consume more salt when they grazed with their mothers when lambs on a plant community with moderate to low Na content (Montes, 2016). Thus, when experienced yearlings were exposed to medusahead and tall fescue hay, they likely increased their Na intake relative to inexperienced yearlings to balance the low Na:K ratio found in grasses like tall fescue (i.e., 24.5 g K and 0.12 g Na/kg DM; Swift et al., 2007) and medusahead (i.e., 12.0 g K/kg DM; Bovey et al., 1961). Hubbert et al. (1958) reported that it appeared desirable to maintain a ratio between the concentration of sodium and potassium for maximum cellulose digestion on *in vitro* trials. For instance, according to NRC's sheep requirements (2007), the required Na:K ratio for growing sheep is 1:1.65. Additionally, fertilization of perennial ryegrass (*Lolium perenne*) with sodium increased DM digestibility, while it increased Na content, decreased K content, with no apparent change in CP and fiber concentrations in the plant's tissues (Chiy and Phillips, 1998). Sheep fed alfalfa tended to eat less trace-mineralized salt blocks than sheep that did not receive this forage. Alfalfa hay supplied some of the yearlings' trace-mineral requirements (i.e., Zn; NRC, 2007), which likely led to a reduction in the use of trace-mineralized blocks by supplemented animals.

4.3. Animal performance

During Experiment 1, experienced animals tended to gain more weight and showed better gain-to-feed ratio than inexperienced animals. Consistent with these findings, lambs exposed to low-quality roughages early in life showed greater *in vivo* digestibility values when fed a different low-quality forage later in life than lambs without such early experience (Distel et

al., 1994). Likewise, beef cows exposed to a low-quality forage early in their lives had a better body condition score, body weight and reproductive parameters than inexperienced animals when fed the same low-quality forage later in life (Wiedmeier et al., 2002). Early exposure of mammals to different feeds and locations may lead to changes in gene expression, which allow for a better adaptation to the animal's local feeding environment (Provenza, 2008).

Minerals also have an important role in body weight gains. Croom et al. (1982) and Rossi et al. (1998) reported that NaCl could increase feed efficiency in ruminants. Sodium forms part of diverse transport systems (i.e., Na/K pump) that are important in glucose and amino acid uptake by tissues, maintenance of body temperature, neuromuscular activation, and nerve function (NRC, 2007). Experienced yearlings tended to consume more salt than inexperienced yearlings, which could have contributed to the differences in BW and gain-to-feed ratio found between groups.

During Experiment 2, all animals lost weight and early experience with grazing medusahead did not influence this variable. The poor quality of the plant community compounded with the greater maintenance requirements for animals under grazing conditions (Owens et al., 1993; Van Soest, 1994) may have contributed to this outcome, which likely overrode the positive effects of early experience on BW gains found during Experiment 1.

4.4. Use of medusahead on rangeland

Animals become averse to foods eaten too frequently or in excess; the more of any particular food an animal eats, the greater the aversion to the food. The degree to which a food is avoided following a meal depends on such excessive exposure compounded with the presence of toxins in the food or with the occurrence of nutrient imbalances (Provenza, 1996). It is likely that yearlings became averse to medusahead due to the excessive exposure they received to this silica accumulator weed during Experiment 1. This resulted in the almost nil use of medusahead observed during grazing in Experiment 2. Yearlings were observed grazing medusahead for only 0.44% of the events recorded during scan sampling, which contrasts with

the value of 4.4% recorded when they grazed medusahead-infested rangeland with their mothers when lambs (Montes, 2016).

At the beginning of the grazing experiment, the use of forbs, bunch grasses, and annual grasses by yearlings was proportional to their abundance; however, as days elapsed sheep changed the use of different plant functional groups with a gradual reduction in forb defoliation – a preferred component of the vegetation that declined in abundance - and an increase in the use of grasses. It has been observed that grazing animals change their diet selection in an attempt to rebalance the ingestion of nutrients as a function of their changing requirements (Parsons et al., 1994).

5. Conclusions

The low and cyclic intake of medusahead showed by yearling sheep and the growth of medusahead in patches can be used as the basis for prescribed grazing in medusahead-infested rangeland. Animals may be managed to grazing cycles where they are concentrated in medusahead-infested patches for a short period of time (i.e., 1 day), moved to a diverse vegetation for 3-7 days, and then returned to medusahead patches for another short period of time. This rotation will make a more efficient use of the weed, as it will mimic the described cyclic pattern of medusahead intake by sheep exposed to *ad libitum* amounts of this weed. In addition, experienced animals in this context may use medusahead more evenly and display better BW gains than inexperienced animals. Nevertheless, it is worth mentioning that the proposed management approach should be avoided during the period of seed disarticulation, thus preventing the potential long-distance dispersal of medusahead seed via epizoochory. Animals previously forced to graze medusahead, even if they consumed the weed early in life with their mothers, may display a much lower use of the weed as shown in this study. Experienced sheep also showed a greater intake of NaCl, which could be explained by their early experiences with grazing a plant community likely poor in Na.

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Figure captions

Fig. 1. Average daily dry matter (DM) intake of medusahead by four groups of yearling sheep during 3-h of exposure in pens (Experiment 1). (A) Average daily intake of medusahead across the four groups (day effect; $P < 0.0001$): with (Experience) or without (Inexperience) early experience at grazing medusahead-infested rangeland and with (alfalfa) or without (no alfalfa) alfalfa hay availability. (B) Average daily intake of medusahead across the 2 levels of alfalfa availability (alfalfa, no alfalfa) by sheep with and without experience at grazing medusahead-infested rangeland (experience $\times$ day effect; $P = 0.036$). Values are means with SEM. Means with the same letter did not differ ($P > 0.05$) between days (A) or between groups on different days (B).

Fig. 2. Intake of salt (NaCl) and trace-mineralized salt blocks (NaCl + microminerals [Zn, Mn, Fe, Cu, I, and Co]) by sheep measured every 2 days (Experiment 1). Values are means with SEM across four groups of animals: with or without early experience at grazing medusahead-infested rangeland and with or without alfalfa hay availability. For each salt block across days: * $P < 0.01$; ** $P < 0.0001$, and means with the same letter did not differ ($P > 0.05$).

Fig. 3. Proportion of total grazing events and grazing events on different functional groups by sheep grazing on medusahead-infested rangeland during 3.5 h of scan sampling (Experiment 2). Values are means with SEM across two groups of animals: with or without early experience at grazing medusahead-infested rangeland. Annual grasses group includes annual grasses other than medusahead. For each event across days: * $P < 0.01$; ** $P < 0.0001$; n.s. = not significant, and means with the same letter did not differ ($P > 0.05$).

Table 1

Chemical composition of the forages fed during Experiment 1 (May 28 to June 6, 2014).

Forage	Content (g/kg dry matter)				
	Crude protein	Neutral detergent fiber	Acid detergent fiber	Ash	Acid insoluble ash
Medusahead					
Day 1, May 28	89.4	613.5	308.3	167.9	108.9
Day 4, May 31	100.6	616.5	303.2	154.6	100.3
Day 7, June 3	91.4	589.2	302.8	170.4	109.9
Day 10, June 6	70.8	641.7	331.6	179.5	107.5
Alfalfa hay	197.1	464.8	340.3	93.1	23.0
Tall fescue hay	153.3	607.1	301.6	104.1	32.4

Chemical analyses of 1 replicate

Table 2

Chemical composition (mean $\pm$ SEM) of the plant community where sheep grazed medusahead-infested rangeland from June 9 to June 19, 2014 (Experiment 2).

Plant group	Content (g/kg dry matter)				
	Crude protein	Neutral detergent fiber	Acid detergent fiber	Ash	Acid insoluble ash
Pre-grazing (June 9, 2014)					
Medusahead	96.2 $\pm$ 6.8 ^{ab}	623.1 $\pm$ 2.5 ^{ab}	305.2 $\pm$ 4.7 ^{ab}	128.4 $\pm$ 6.1 ^a	82.0 $\pm$ 7.9 ^a
Annual grasses*	84.5 $\pm$ 1.3 ^{bc}	575.8 $\pm$ 1.1 ^b	292.5 $\pm$ 3.7 ^a	76.6 $\pm$ 3.6 ^{cd}	36.6 $\pm$ 0.6 ^b
Bunch grasses	71.7 $\pm$ 5.3 ^c	687.4 $\pm$ 11.3 ^{ac}	312.3 $\pm$ 2.2 ^{ab}	77.0 $\pm$ 2.9 ^{cd}	38.7 $\pm$ 3.3 ^b
Forbs	102.2 $\pm$ 4.2 ^a	376.0 $\pm$ 9.9 ^d	258.1 $\pm$ 5.3 ^c	103.3 $\pm$ 2.3 ^b	5.4 $\pm$ 0.8 ^c
Post-grazing (June 19, 2014)					
Medusahead	71.5 $\pm$ 3.7 ^{ab}	645.1 $\pm$ 4.7 ^a	323.8 $\pm$ 6.0 ^{bd}	101.4 $\pm$ 1.7 ^b	80.6 $\pm$ 7.9 ^a
Annual grasses*	59.2 $\pm$ 1.1 ^{bc}	676.0 $\pm$ 24.2 ^{ac}	351.7 $\pm$ 13.2 ^{de}	67.3 $\pm$ 6.2 ^d	38.3 $\pm$ 6.0 ^b
Bunch grasses	49.9 $\pm$ 4.6 ^c	737.4 $\pm$ 23.9 ^c	402.8 $\pm$ 12.5 ^e	68.9 $\pm$ 7.9 ^d	43.4 $\pm$ 2.8 ^b
Forbs	80.5 $\pm$ 4.8 ^a	373.7 $\pm$ 2.2 ^d	256.4 $\pm$ 1.3 ^c	98.2 $\pm$ 3.2 ^{cb}	7.2 $\pm$ 0.3 ^c
Factor effect					
<i>P</i> -value					
Plant group (P)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Sampling date (S)	< 0.0001	0.0005	< 0.0001	0.0016	n.s.
P $\times$ S	n.s.	0.0073	0.0002	n.s.	n.s.

Chemical analyses of 3 spatial replicates

*This group included annual grasses other than medusahead

Values within a column with same superscripts did not have difference ($P > 0.05$)

n.s. Not significant