



## Using Targeted Grazing to Close the Phenological Niche Exploited by Invasive Annual Bromes

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### ABSTRACT

Phenological differences between native and invasive plants can facilitate invasion, but can also be targeted by management. In the western Great Plains of North America, the invasive annual grasses *Bromus tectorum* L. (cheatgrass) and *B. arvensis* (field brome) begin and end growth earlier than native competitors, providing an opportunity for targeted grazing. However, managers need to know when grazers preferentially consume or avoid annual bromes. We implemented spring targeted grazing for 4 years and quantified temporal cattle consumption patterns at two mixedgrass prairie sites in Wyoming and Nebraska, USA. We used fecal DNA metabarcoding to measure consumption of annual bromes and co-existing native species twice per week. Concurrently, we measured plant phenology, forage quality, and biomass. Within years, brome consumption was predicted effectively using two phenological metrics—plant height and days after seed maturation. Targeted grazing windows, defined as periods with  $\geq 75\%$  of maximum cattle consumption within a year, started when bromes were 9.3 cm ( $\pm 3.6$  SD) tall, ended one day ( $\pm 4$  SD) after seed maturation, and lasted 38 d ( $\pm 11$  SD). Cattle diet quality remained high throughout these grazing windows. Across years, brome consumption ranged from 19% to 55% of total graminoid consumption, and was consistently higher in years when annual bromes grew taller before flowering. Although cattle typically selected for native perennials over annual bromes, spring targeted grazing reduced brome seed production by 30–77% relative to adjacent pastures where grazing began later. These results indicate that simple phenological metrics can predict cattle consumption of bromes during spring, both within and among years. Carefully timing grazing to align with consumption should help managers to control annual bromes and restore native mixedgrass prairie plant communities. More broadly, combining temporal analyses of livestock diets and plant phenology can be useful for precisely targeting grazing of invasive species.

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### Introduction

Phenology plays an important role in plant competition by defining the timing of plant resource acquisition and exposure to environmental stress. Invasive plants can gain advantages over native competitors if their phenology allows them to grow and reproduce when the risk of herbivory is lower, or to acquire resources at times when native species are inactive (Wolkovich and Cleland 2011). For example, access to soil resources after native species enter dormancy has contributed to the success of invasive Amur honeysuckle (*Lonicera maackii*) in forests of the eastern US and invasive

knapweeds (*Centaurea* spp.) in western US rangelands (Wolkovich and Cleland 2011).

Open phenological niches are often exploited by invasive annual plants, including *Bromus tectorum* L. (cheatgrass) and *B. arvensis* L. (field brome), hereafter, annual bromes. These annual grasses have invaded millions of hectares of North American rangelands (Bradley 2009; Boyte and Wylie 2016; Kleinhesselink et al. 2023), replaced productive perennial forage species (Knapp 1996; Haferkamp et al. 2001a; Haferkamp et al. 2001b; Ogle et al. 2003), increased fire frequency (D'Antonio and Vitousek 1992; Balch et al. 2013), and reduced native species diversity (Melgoza et al. 1990; Ashton et al. 2016). Annual bromes initiate growth before many native perennial plant species in their invaded ranges, facilitating earlier access to water and nutrients (Melgoza et al. 1990; Kulmatiski et al. 2006; Concilio et al. 2017). Coupled with their

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rapid resource acquisition and growth rates, the earlier phenology of annual bromes can give them a competitive advantage over native perennials.

As climate change proceeds, increasing temperatures are likely to expand early season phenological niches and further accelerate annual brome invasion in North America (Bradley 2009). Particularly in cooler environments, annual brome growth is limited by low winter-spring temperatures (Bradley 2009; Bradley et al. 2016), and warming can greatly increase the ability of bromes to grow when native species are inactive (Zelikova et al. 2013; Compagnoni and Adler 2014; Blumenthal et al. 2016). In the northern Great Plains, predicted increases in cool-season precipitation may also favor annual bromes over native plants (Zelikova et al. 2013; Prevey and Seastedt 2014; Concilio et al. 2017).

Although phenological niche separation between invasive and native plants can facilitate invasion, it also presents opportunities for targeted management (Marushia et al. 2010; Wolkovich and Cleland 2011; Bennett et al. 2019; Hendrickson et al. 2020; Symstad et al. 2021). In ecosystems where invasive and native species coexist, management applied when invasive plants are more vulnerable than native plants can alter the balance of competition in favor of natives. One phenologically-based approach that holds promise for controlling annual bromes is early spring targeted grazing. Grazing can inhibit annual bromes through 1) defoliation, which limits seed production, 2) direct consumption of flowers/seeds, or 3) litter reduction, which can reduce brome establishment (Perryman et al. 2020; Reinhart et al. 2020; Waterman and Vermeire 2021).

Early spring targeted grazing may work particularly well in the western Great Plains of North America, where the long summer growing season of native perennial plants creates substantial phenological niche separation between annual bromes and native species (Wolkovich and Cleland 2011; Prevey and Seastedt 2014). This is in contrast with the Intermountain West, where the growing seasons of native perennial plants and annual bromes overlap more (Booth et al. 2003; Chambers et al. 2007; Brooks et al. 2016). In addition, native graminoids of the western Great Plains are well-adapted to grazing, due to an evolutionary history of grazing by native ungulates (Mack and Thompson 1982; Milchunas et al. 1988). The combination of distinct phenology and grazing adaptations may allow native plant communities in the western Great Plains to recover following spring targeted grazing, while also benefitting from reductions in annual brome populations.

For a targeted grazing strategy to succeed, the timing, duration, and stocking rate must be precisely defined (Bailey et al. 2019). Timing is a critical detail—the same grazing strategy applied at the wrong time can exacerbate invasion, rather than help to control the invader and restore desired native species (Rinella and Hileman 2009). For annual brome control, targeted grazing should occur when bromes are both accessible and palatable to grazers (Launchbaugh and Walker 2006; Rinella and Hileman 2009), while also minimizing effects on native perennial plants. The timing of this period shifts from year to year, however, with variation in annual brome germination, growth, and flowering phenology (Mack and Pyke 1983; Chambers et al. 2007; Bradley et al. 2016), each of which can influence grazing animal selection and preference (Hodgson et al. 1994; Harmoney 2007). Targeted grazing has shown potential to reduce annual brome abundance (Mosley and Roselle 2006; Harmoney 2007; Diamond et al. 2012; Davies et al. 2021a; Porensky et al. 2021; Vermeire et al. 2023) and increase native species abundances (Schmelzer et al. 2014; Porensky et al. 2021), but the approaches and outcomes, especially over longer timeframes, have varied widely. To improve the likelihood of successful annual brome control, it is necessary to precisely identify the temporal windows within which grazers will maximize con-

sumption of annual bromes, and selection for annual bromes relative to native perennials.

We used a novel approach to quantify temporal patterns of cattle consumption of the annual brome species *B. tectorum* and *B. arvensis*. Our study took place at two mixed-grass prairie sites in the western Great Plains over 4 years. Within experimental spring grazing pastures, we sampled fecal material twice per week and used differences in chloroplast DNA signatures to determine the quantity of different species in cattle diets (Bergmann et al. 2015; Jorns et al. 2020; Craine 2021; Jorns et al. 2023). While this method cannot always distinguish between closely related species (Scasta et al. 2019), the distinct chloroplast sequences of annual bromes allowed us to estimate the proportion of annual bromes relative to other grass species in the diet. Concurrently with diet tracking, we measured phenology, forage quality, and biomass of both annual bromes and coexisting native plant species to better understand how these factors influence cattle selection. We asked the following questions: 1) Can we predict cattle consumption of annual bromes and selection for annual bromes relative to native perennial grass species from plant phenology or forage quality? 2) Which years, as defined by annual brome phenology or forage quality, are best suited for targeted grazing of annual bromes? 3) How does spring targeted grazing influence annual brome seed production and cattle weight gain?

## Materials and Methods

### Study areas

Our study occurred at two mixed-grass rangeland sites, the first near Scottsbluff, Nebraska (University of Nebraska-Lincoln Panhandle Research, Extension, and Education Center: latitude 42°01'N, longitude 103°44'W, 1270 m elevation), hereafter “NE”, and the second near Cheyenne, Wyoming (USDA-Agricultural Research Service High Plains Grasslands Research Station: latitude 41°12'N, longitude 104°51'W, 1920 m elevation), hereafter “WY”, USA. Mean annual air temperature is 9.5°C at NE, and 8.0°C at WY. Mean annual precipitation is 404 ± 111 mm [SD] at NE (1981–2020, GHCND: USW00024028), and 403 ± 75 mm [SD] at WY (1981–2020, GHCND: USW00024018). At NE, the plant community is composed of cool-season ( $C_3$ ) perennial grasses (mainly *Hesperostipa comata*, needle and thread, *Pascopyrum smithii*, western wheatgrass, and *Achnatherum hymenoides*, Indian ricegrass) and warm-season ( $C_4$ ) perennial grasses (*Calamovilfa longifolia*, prairie sandreed, and *Bouteloua gracilis*, blue grama), with a minor component of forbs and subshrubs. The WY site is dominated by cool-season perennial graminoids (including *H. comata*, *P. smithii*, and *Carex duriuscula*, needleleaf sedge), with smaller amounts of warm-season grasses (primarily *B. gracilis*), forbs and subshrubs. *Bromus tectorum* and *B. arvensis* co-occur at the WY site, while only *B. tectorum* is present at NE. In WY, *B. tectorum* accounted for approximately 86% of total annual brome cover during the four study years, as estimated from long-term vegetation transects adjacent to the study site (Porensky et al. 2016).

In NE, the soils include a Valent fine sand and Valent loamy fine sand (mixed mesic Ustic Torripsamments), and in WY, soils include an Ascalon variant loam and Altvan sandy loam (fine-loamy mixed mesic Aridic Argiustolls). Prior to the study, both sites had been subjected to season-long grazing as follows: in NE, the pasture area had been used for season-long continuous grazing with an average stocking rate of 30 animal unit days per hectare [AUD · ha<sup>-1</sup>; mean ± SD]. In WY, the pasture received continuous, season-long (early June–early October) grazing at a light stocking rate (15.7 ± 2.8 AUD · ha<sup>-1</sup>; for more details see Porensky et al. 2016). Pronghorn (*Antilocapra americana*) were also present at both sites.

## Experimental design

We mapped vegetation communities dominated by annual bromes at each study site in 2016, prior to study initiation, using a handheld GPS unit with submeter accuracy (Trimble GeoExplorer GeoXT 2008 Series, Sunnyvale, CA). Vegetation was classified as brome-dominated if it contained  $\geq 50\%$  *Bromus* spp. aerial cover, determined when annual bromes were near maximum cover and most visually distinct relative to surrounding vegetation (flowering, red phenological phase). At each site, a 4-hectare experimental pasture was established and fenced off from the surrounding pasture based on mapped vegetation to include approximately 50% brome-dominated communities and 50% native mixed-grass communities (Fig. S1). Native communities also commonly included sub-dominant (non-zero) cover of *Bromus* spp., and vice versa for brome-dominated communities.

From 2017 to 2020, each study pasture was grazed yearly by three to four Angus/Angus cross yearling heifers between mid-April (DOY 107–121) and late June or early July (DOY 174–197), coincident with the period when annual bromes were actively growing. Weather permitting, grazing was timed to encompass the entire period from plant growth initiation through the end of annual brome senescence. This led to variation in the duration of the grazing period, with 2019 being longer (80 and 84 d, in NE and WY) than other years (56–60 d and 54–66 d, respectively). Cattle were fed supplemental hay (not including *Bromus* species) on rare occasions when snow cover prevented pasture grazing (NE: DOY 120–121 in 2019; WY: DOY 111 and 138–140 in 2017, and DOY 120–121 in 2019). Pasture stocking density was determined from previous work at each study site, starting with four yearlings at each site in 2017, and was adjusted to three yearlings in WY in 2018–2020 to account for lower observed productivity. In addition, due to difficulty replacing an escaped animal, stocking density was limited to three yearlings in NE throughout the grazing period in 2017. Plant biomass was measured in the presence of grazing, and was similar at the WY site with three yearlings and the NE site with four yearlings. Differences in stocking density combined with variation in grazing period duration to yield variable, moderate to heavy stocking rates:  $41.8 \pm 5.4$  SE AUD  $\cdot$  ha<sup>-1</sup> in NE, and  $37.0 \pm 4.7$  SE AUD  $\cdot$  ha<sup>-1</sup> in WY. Cattle were weighed at the start and end of each targeted grazing season at the WY site to provide additional management context. Mean cattle starting weights ( $\pm$  SD) for 2017–2020 were as follows: 263  $\pm$  4 kg, 318  $\pm$  15 kg, 318  $\pm$  4 kg, 284  $\pm$  9 kg.

## Plant measurements

Plant phenology was recorded twice per week at each study pasture for 10 marked individuals of *B. tectorum*, and 5–10 individuals each of *P. smithii* and *H. comata*. We focused on ungrazed plants adjacent to the study pasture because they provided a readily observable barometer of population-level phenology. While the phenology of ungrazed plants was generally representative of population-level phenology, we note that grazing can influence phenology (i.e., by keeping some plants in a vegetative state for longer periods). On each observation date, we measured plant height, and assessed flowering stage ([1] flower formation: flowers developing or “in the boot”, and [2] flowering: open, mature flowers with florets fully emerged) and seed maturity (indicated by seeds being firm and resistant to bending). A plant was considered to have reached a specified phenological stage when  $\geq 50\%$  of its flowers or seeds reached that stage.

To determine effects of forage quality on cattle selection, we sampled plant tissue of *B. tectorum*, *H. comata*, and *P. smithii* throughout each study pasture once per week. Each tissue sample included a range in phenological stages for each species on

each collection date, to represent what was available to cattle. Previous years' (standing dead) tissue was removed. Tissue was oven-dried at 55°C, ground, and analyzed by species for crude protein, fiber, and micronutrient contents via near-infrared reflectance spectroscopy (NIRS) at Ward Laboratories (Kearney, NE) (Stuth et al. 2003). Total digestible nutrients, a measure of forage energy value (Mathis and Sawyer 2007), was calculated by the laboratory using calibrated relationships among TDN and in-vitro measured digestibility, crude protein, fiber, and non-fibrous carbohydrate contents. For data analysis, we focused primarily on crude protein (rather than total digestible nutrients, which provided similar information; Fig. S4), on the assumption that protein would be most limiting to cattle in spring.

To quantify changes in forage availability, we harvested above-ground biomass at 30 (NE) or 60 (WY) fixed sampling locations distributed throughout each pasture once per two week period. Sampling locations were stratified across the two vegetation community types (annual brome-dominated and native mixed-grass) to ensure that the proportion of locations within each community type matched the proportion of the pasture covered by that community. Twice as many locations were sampled at the WY site due to higher spatial heterogeneity of vegetation patches. At each sampling location a 2 m x 2 m plot was permanently marked. On each sampling date, all biomass was harvested to ground level from within a 20 cm x 50 cm subplot, with each subplot measured only once per year. Biomass was separated into (1) annual bromes, (2) dominant cool-season perennial grass species *H. comata* and *P. smithii*, (3) all other graminoid species, and (4) forbs, and oven-dried at 60°C to constant weight prior to weighing.

At each site, we measured the effect of early spring grazing on annual brome seed production once each year by harvesting 15 pairs of 20 cm x 50 cm plots, with each pair containing one plot inside and one outside the study pasture (1–2 m from the fence). Plots were co-located within mapped brome-dominated vegetation patches, and spatially distributed around the entire pasture perimeter. Plots outside the fence lines were not grazed by cattle during April and May, but did experience summer grazing (June–late September) at light stocking rates. We conducted seed biomass harvests when annual brome seeds were maturing but not yet detached. To determine the timing of seed biomass harvests, we assessed flower and seed maturity from seed firmness and floret color for 30 randomly selected plants within each pasture. Harvest dates ranged from 13 June to 8 July (DOY 164–190) at NE, and 11 June to 1 July (DOY 164–182) at WY. Following harvest, we first separated biomass into non-brome and brome components, and, for bromes, we separated seed mass from total biomass. Seed harvest plots were not true replicates and therefore cannot be used to rule out the possibility that differences in seed production were caused by the pasture location rather than grazing management. However, we consider this possibility unlikely given that plant communities were similar and management was identical within and outside of the two study pastures prior to the study, and harvest plots were widely distributed around pasture perimeters.

## Cattle diet quality and composition

To assess cattle diet quality and composition, we sampled fresh fecal pats twice per week at both sites. On each collection date, fecal pat samples from two to four study animals were collected immediately following defecation, composited, thoroughly mixed, and frozen until the time of analysis. Diet quality was measured at weekly intervals by analyzing the first of the two weekly fecal samples. Frozen samples were sent to the Grazing Animal Nutrition Lab (Texas A&M, Temple, TX, USA) where they were analyzed with NIRS to determine fecal crude protein, digestible organic matter, nitrogen, and phosphorous contents.

We sequenced chloroplast DNA extracted from the two fecal samples per week to estimate cattle consumption of dominant plant species and determine when cattle selected annual bromes in higher/lower proportion relative to cool-season perennial grasses. DNA extraction, amplification, and sequencing was performed by Jonah Ventures Laboratory (Boulder, CO, USA). To facilitate metabarcoding, a fragment of the chloroplast *trnL* intron was targeted and amplified with the c-h primers (as explained by Taberlet et al. 2007, and applied by Craine et al. 2015, Craine 2021). DNA sequencing was conducted on an Illumina MiSeq running 2 × 150 bp chemistry with a v2 300-cycle kit (for more details, see Jorns et al. 2020 and Craine 2021). Sequencing produced read counts of exact sequence variants (ESVs) (Callahan et al. 2017), and the proportion of diet attributed to each ESV was calculated as number of ESV reads per total reads in each sample. These results represent the proportional protein contribution of each ESV to cattle, which approximates the associated proportion of biomass consumed by cattle (Craine et al. 2015).

#### Assignment of plant taxonomy to ESV data

To assign taxonomic identity to ESVs in fecal samples, we first constrained the pool of potential species matches using lists of plant species observed at each study site. Individual species can be represented by multiple ESVs due to natural intraspecific variation of the targeted genomic region or errors in PCR amplification. We identified a consensus sequence for each plant species to use as a baseline comparison for all ESVs identified in fecal samples. Consensus sequences were identified by cross-referencing ESVs found in multiple fecal samples with sequences from individual plant species collected at our study sites and sequences found in NCBI's GenBank database (Appendix A). To determine the most likely taxonomic identity of each ESV, we performed pair-wise alignment between all consensus sequences and all fecal sample sequences using the NCBI BLAST algorithm tool (adjusted to account for mismatched extensions outside of the initial alignment region; Appendix A). Only ESVs with at least 95% similarity to a consensus sequence were retained for analysis. Of the dominant focal species (*B. tectorum*, *B. arvensis*, *H. comata*, and *P. smithii*), only *P. smithii* had close relatives within the species lists that could not be differentiated by their chloroplast genetic signatures. However, these two close relatives (*Vulpia octoflora* and *Koeleria macrantha*) were minor components of available forage and unlikely to contribute meaningfully to cattle diet.

Taxonomic assignments identified 95% (± 6% S.D.) of the ESVs in each fecal sample (Appendix A). At both study sites, we observed very high read counts of ESVs identified as uncommon forb species. We suspect that a methodological artifact may cause ESVs of certain indigestible forb species to occur at higher frequency in the fecal sample than in the diet. Other fecal DNA studies have reported discrepancies in expected diet composition (Scasta et al. 2019), particularly with respect to higher than expected abundances of some forb species (King and Schoenecker 2019; Jorns et al. 2020). To prevent this potential artifact from causing spurious patterns in relative consumption of annual bromes, we calculated the proportion of annual bromes relative to all graminoids in cattle diets. Graminoids make up 81% and 95% of total plant biomass in the WY and NE pastures, respectively.

## Analysis

### Data summary

We summarized the phenology of flowering and seed maturation by identifying the days on which ≥ 50% of the 10 marked plants had open, mature flowers or firm seeds, respectively, for

each site and year. From these dates, we calculated the continuous metrics “days after flowering” and “days after seed maturation,” which included both negative (before 50% flowering or firm seeds) and positive values (after 50% flowering or firm seeds).

To temporally align the phenology and forage quality sampling dates with the diet composition data, we assumed 72 h between forage consumption and passage through the digestive system (Waldo et al. 1972). We therefore paired fecal sample composition with forage quality or phenology measured 3 d prior (or determined via linear interpolation between the two dates closest to 3 d prior).

### Data analysis

To understand how targeted grazing influences mixed-grass prairie plant communities, we focused on two response variables: 1) brome consumption as a proportion of graminoid species in cattle diet (hereafter, “brome consumption”), and 2) brome selection, adjusting for the availability of both bromes and other graminoids in the pastures (“brome selection”). We focus primarily on brome consumption, on the assumption that the amount of brome removed through grazing is likely to determine brome control. For other management objectives, however, such as the recovery of cool-season perennial grasses, cattle consumption of bromes and other species relative to their abundance within the plant community (selection) may be more useful. Consumption relative to abundance is also useful for comparisons across years and sites with differing brome abundance. We calculated cattle selection as (Eq. 1):

$$\frac{(\% \text{ of species } X \text{ in diet} - \% \text{ of species } X \text{ in biomass})}{(\% \text{ of species } X \text{ in diet} + \% \text{ of species } X \text{ in biomass})} \quad (1)$$

where species percentages were determined relative to the proportion of all graminoids present in the diet and biomass (Odadi et al. 2013). Selection index values range from -1 (total avoidance) to 0 (no selection) to 1 (total selection).

We used model selection to determine the combination of phenological and forage quality variables that best predicted brome consumption and selection. The model set for brome consumption contained 19 candidate models (Table 1). Our null model included a fixed effect of site and a random effect of site-year (to account for covariation among measurements from the same site and year). Five models added one of the following individual fixed effects to the null model: plant height (indicating early season accessibility), days after flowering (indicating early maturity), days after seed maturation (indicating full maturity), crude protein content (indicating forage quality), and day of year (to test whether plant phenology or forage quality were more informative than calendar date). Four additional models included effects of plant height in combination with either days after flowering, days after seed maturation, crude protein, or day of year, along with the corresponding interaction. The last four variables were collinear with one another and were therefore not included together in the same models. We considered each of the above nine models with and without brome percentage of total graminoid biomass at the time of sampling as a covariate (hereafter, “brome availability”) to determine whether accounting for brome abundance improved prediction of brome consumption. Analysis of cattle selection for brome matched that for brome consumption described above, but omitted models that included brome availability, which is already incorporated into the selection index (Table S3).

For all model selection analyses, we selected the models that minimized Akaike's Information Criterion adjusted for limited sample sizes (AICc; Tables 1 and S3). All analyses were conducted in R (R Core Team 2013) using the lmer() function of the 'lme4' package (Bates et al. 2020). Explanatory variables were centered and then

**Table 1**  
Model selection to predict cattle brome consumption.

MODEL	K	LogLik	AICc	$\Delta$ AICc	$w_i$	R <sup>2</sup> cond.	R <sup>2</sup> marg.	Significant factors
Ht x SM + BrAv	7	86.74	-158.65	0.0	0.937	0.63	0.49	<b>Ht***, SM***, BrAv***, Ht x SM***</b>
Ht x SM	6	82.82	-153.03	5.6	0.056	0.53	0.42	<b>Ht***, SM***, Ht x SM***</b>
Ht x FD + BrAv	7	81.75	-148.66	10.0	0.006	0.67	0.40	<b>Ht***, FD***, BrAv***, Ht x FD***</b>
Ht x DOY + BrAv	7	78.11	-141.38	17.3	2E-04	0.79	0.43	<b>Ht***, DOY***, BrAv***, Ht x DOY***</b>
Ht x FD	6	76.24	-139.87	18.8	8E-05	0.54	0.30	<b>Ht***, FD***, Ht x FD***</b>
Ht x CP + BrAv	7	74.40	-133.97	24.7	4E-06	0.54	0.41	<b>Ht***, CP***, Ht x CP***, BrAv**</b>
Ht x CP	6	72.19	-131.76	26.9	1E-06	0.48	0.34	<b>Ht***, CP***, Ht x CP***</b>
Ht x DOY	6	69.14	-125.67	33.0	6E-08	0.53	0.28	<b>Ht***, DOY***, Ht x DOY***</b>
SM + BrAv	5	63.22	-116.00	42.7	5E-10	0.60	0.22	<b>SM***, BrAv***</b>
FD + BrAv	5	62.87	-115.30	43.4	4E-10	0.62	0.21	<b>FD***, BrAv***</b>
DOY + BrAv	5	62.65	-114.86	43.8	3E-10	0.64	0.23	<b>DOY***, BrAv***</b>
Null	3	58.68	-111.19	47.5	5E-11	0.36	0.00	<b>Intercept***</b>
CP + BrAv	5	60.09	-109.74	48.9	2E-11	0.56	0.18	<b>CP*, BrAv***</b>
SM	4	57.56	-106.84	51.8	5E-12	0.36	0.02	<b>SM*</b>
DOY	4	57.33	-106.37	52.3	4E-12	0.37	0.02	<b>DOY*</b>
FD	4	57.24	-106.20	52.5	4E-12	0.38	0.02	<b>FD*</b>
Ht + BrAv	5	57.56	-104.68	54.0	2E-12	0.56	0.15	Ht, <b>BrAv**</b>
CP	4	55.97	-103.65	55.0	1E-12	0.35	0.01	CP
Ht	4	55.34	-102.39	56.3	6E-13	0.35	0.00	Ht

Models incorporated fixed effects for plant height (Ht), days after flowering (FD), days after seed maturation (SM), crude protein content (CP), and day of year (DOY), with and without a covariate for brome availability (brome percentage of total graminoid biomass, BrAv). Each model included a site-year random effect term. For each model, significant effects are indicated by bold font and noted as \* $p < 0.05$ ; \*\* $p < 0.01$ , \*\*\* $p < 0.001$ . See Table S2 for model coefficient estimates.

scaled relative to the standard deviation. Models used a Gaussian distribution, and data were transformed when necessary to meet assumptions of normality. We used the 'lme4' default unstructured variance-covariance matrix.

To understand how the efficacy of targeted grazing varied among years, we regressed season averages for brome consumption and selection against brome height at the time of flowering, separately for each site. The predictor variable was designed to integrate information about forage accessibility and quality: the total amount of brome available to cattle should be greater in years when it is tall for a long time prior to maturation and the associated decline in forage quality (Mathis and Sawyer 2007). We limited season averages to common sampling dates across sites and years (12 common dates, approximately 5 May–12 June).

## Results

Weather during the annual brome growing season varied widely among years (Table S1 and Fig. S2). Winter-spring (Sep–May) precipitation ranged from 175 to 356 mm and 158–335 mm (67–137% and 64–136% of the long-term average) in NE and WY, respectively. Overall, winter-spring precipitation was higher in 2017 and 2019, and lower in 2020. Precipitation in 2018 was intermediate, as a very dry early spring was followed by wetter conditions in May. Average temperature over the winter-spring months (Sep–May) varied among years from 4.3 to 6.2°C in NE, and 3.7–5.3°C in WY. Phenology and production of bromes and dominant native graminoids also varied markedly among years (Fig. S3).

### Determinants of brome consumption

Of the models explaining brome consumption, the model with lowest AICc included plant height, days after seed maturation, and brome availability (Table 1). This model had strong support relative to alternatives (delta AICc > 5) and the null model (delta AICc = 47.5). Overall, model predictions for brome consumption tracked observed consumption well (Fig. 1B; conditional R<sup>2</sup> = 0.63 and marginal R<sup>2</sup> = 0.49), capturing both the timing of peak consumption and the decline in consumption as annual bromes matured. Brome consumption was initially limited by low brome height, and increased as bromes became taller ( $\beta = 0.16$ ,  $p < 0.001$ ; Table S2). Consumption then decreased with phenological maturation as seeds ripened ( $\beta = -0.2$ ,  $p < 0.001$ ; Fig. 1A). The strong

interaction between plant height and days after seed maturation ( $p < 0.001$ ) indicated that a later seed maturation date increased consumption more once plants became taller. Consumption also increased with greater brome availability ( $\beta = 0.08$ ,  $p < 0.001$ ). In all cases, AICc was lower for models that included brome availability than for the corresponding models without this covariate, indicating that phenology variables were more effective at predicting brome consumption when incorporating information on the relative abundance of bromes.

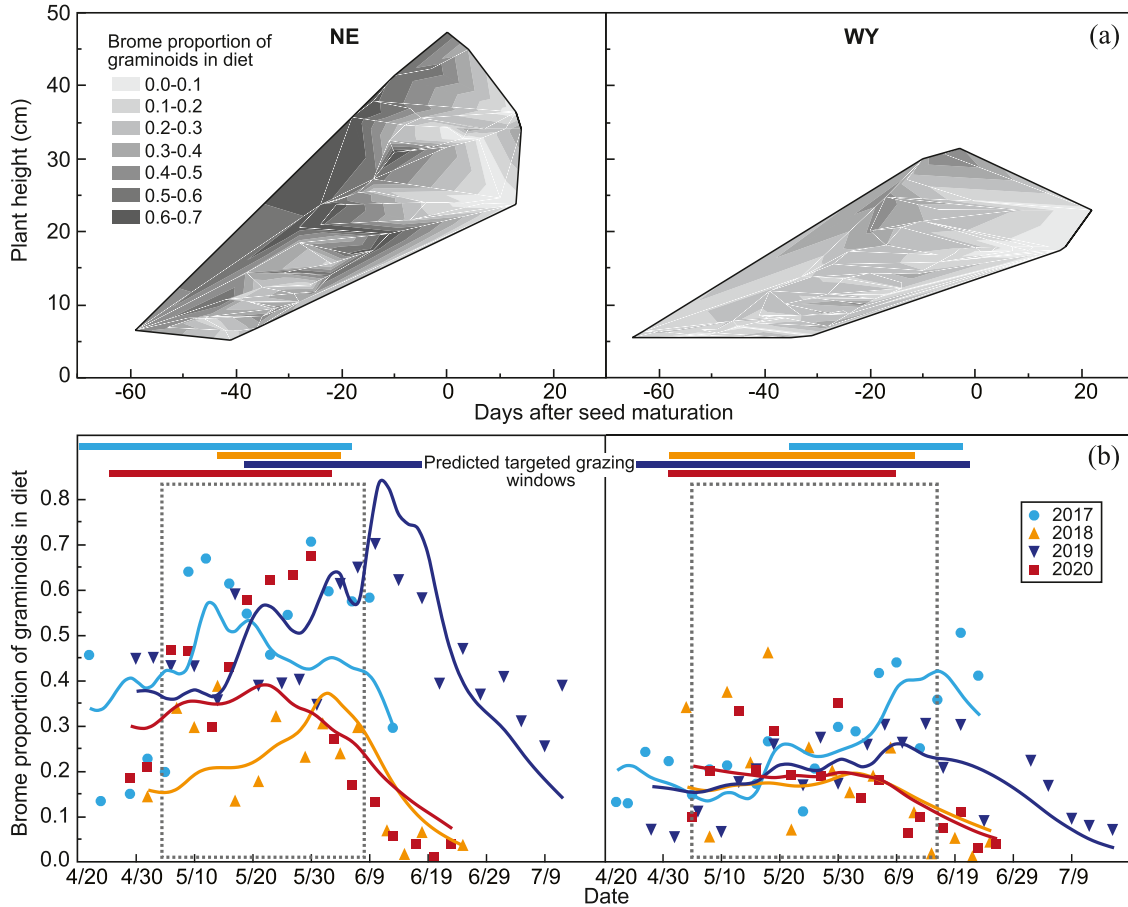
Crude protein of annual bromes declined linearly with days after seed maturation at both sites, in all years (R<sup>2</sup> = 0.81–0.99; Fig. 2), reaching levels expected to limit cattle growth at around the time seeds matured. Nevertheless, model selection revealed that forage quality was less effective in explaining brome consumption than either days after flowering (Table 1, delta AICc between top FD and CP models = 14.7) or days after seed maturation (delta AICc between top SM and CP models = 24.7).

### Identifying targeted grazing windows within years

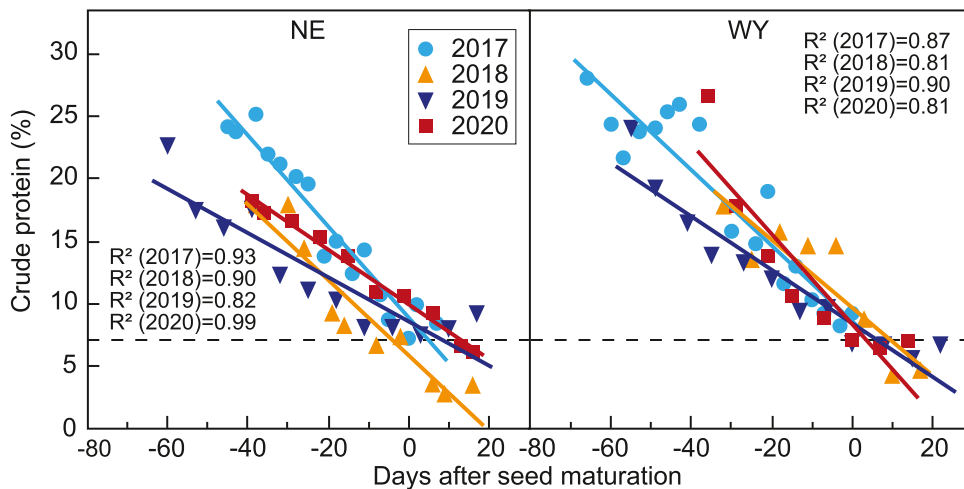
We defined the targeted grazing window in each study year as the period including all dates on which predicted brome consumption was  $\geq 75\%$  of maximum for the growing season (Fig. 1B). On average, these windows started when annual bromes were 9.3 cm tall ( $\pm 3.6$  cm SD) and ended one day after seed maturation ( $\pm 4$  d SD; Fig. 3). The calendar dates on which windows started and ended were more variable than the phenological stages. In NE, the average window started on 4 May (DOY 124;  $\pm 12$  d SD) and ended on 8 June (DOY 159;  $\pm 6$  d SD), with average duration of 35 d. In WY, the average window started on 5 May (DOY 125;  $\pm 10$  d SD) and ended on 16 June (DOY 167;  $\pm 5$  d SD) with an average duration of 42 d. The  $\geq 75\%$  of maximum brome consumption threshold captured much of the effective brome grazing season, but could be adjusted based on manager objectives.

### Cattle selection of bromes relative to native graminoids

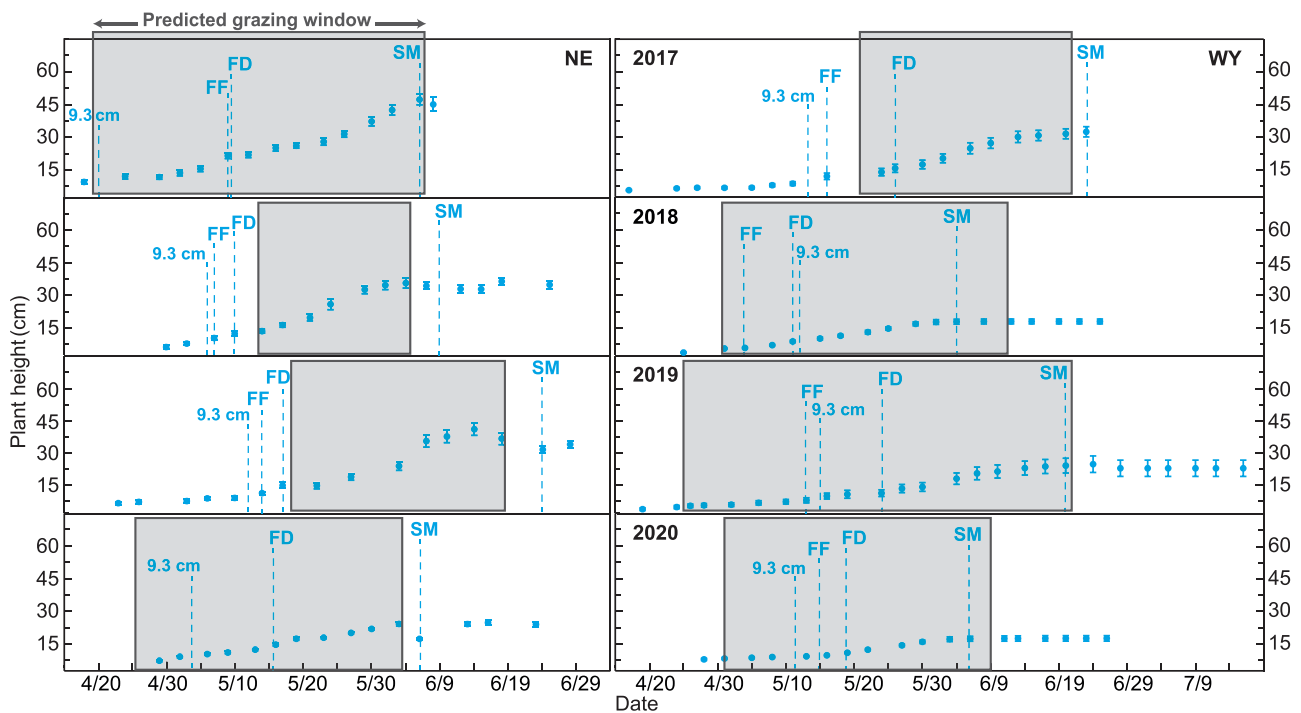
Model selection results for brome selection were qualitatively similar to those for brome consumption with the inclusion of brome availability as a covariate (Table S3). This makes sense, because brome availability is incorporated into both analyses. Cattle selection for annual bromes was best explained by the combination of brome height and days after seed maturation. This



**Figure 1.** (A) Cattle consumption of annual bromes (proportion relative to other graminoids in cattle diet) as a function of plant height and days after seed maturation, across four years at two sites. (B) Observed brome consumption for each year (symbols) with predicted brome consumption (lines) from the model including plant height, days after seed maturation and brome availability (Table 1). Predictions were generated for each date (month/day) on which diet composition was measured. Prediction lines are minimally smoothed splines that pass through the predicted data points (not shown). Across the top of each panel, colored bars indicate predicted targeted grazing windows for annual bromes, which are defined as periods when predicted brome consumption was  $\geq 75\%$  of maximum for each growing season. The average predicted grazing window across years for each site is shown by a dotted gray box.



**Figure 2.** Crude protein declined linearly as annual bromes matured. On the x-axis, 0 represents the date on which  $\geq 50\%$  of observed annual brome plants had mature seeds. The dashed line corresponds with crude protein = 7%, below which energetic costs of digestion become high relative to energy gains (Mathis and Sawyer, 2007), making it more likely that cattle will avoid annual bromes.



**Figure 3.** Predicted grazing windows (gray boxes) overlaid on observed brome height and phenology, including the dates of height = 9.3 cm (9.3 cm), flower formation (FF), flowering (FD), and seed maturation (SM). Grazing windows include all dates when predicted brome consumption was  $\geq 75\%$  of the maximum for each growing season.

top model was substantially better than the next strongest model ( $\Delta \text{AICc} = 10.4$ ) and the null model ( $\Delta \text{AICc} = 42.4$ ). Predicted selection matched observed selection well (Fig. 4; conditional  $R^2 = 0.58$  and marginal  $R^2 = 0.41$ ). As with brome consumption, cattle selection for bromes increased with height ( $\beta = 0.24$ ,  $p < 0.001$ ) and decreased as seeds matured ( $\beta = -0.3$ ,  $p < 0.001$ ). Notably, however, the increase in brome selection with height early in the season was less pronounced than the increase in brome consumption during the same period.

Positive selection for bromes occurred in 2017 (at both sites) and 2019 (particularly in NE), whereas in other study years, cattle consistently selected against bromes. When cattle were not consuming bromes, they selected primarily for *H. comata* throughout the study period, and also increasingly selected for *P. smithii* later in the spring (after 30 May, DOY 150, in 2018 and 2020; and after 19 June, DOY 170, in 2019; Fig. 4). Increased selection for *P. smithii* coincided with increasing avoidance of bromes. Cattle may also have increased selection for common warm-season perennial grass species, such as *Calamovilfa longifolia* in NE and *Bouteloua gracilis* in WY, but these were not measured in the study.

#### Identifying targeted grazing opportunities across years

Both brome consumption and brome selection varied widely between years, even between years with similar overall brome production (e.g., 2018 vs 2019; Figs. 1 and 4). At both sites, cattle selected for and consumed more annual bromes in years when plants grew taller or flowered later. Height at flowering, which integrates these two sources of information, was strongly correlated with seasonal averages of both brome consumption and brome selection (Fig. 5).

#### Associations between brome phenology and weather

To gauge how key brome phenological stages were associated with weather, we explored their relationships with spring temperature and precipitation. In each case, we considered average

**Table 2**

Cattle diet quality during and average daily gain (ADG) following the spring targeted grazing period at the WY site

	2017	2018	2019	2020
CP (%)	11.4 (9.5–12.9)	11.7 (9.4–14.7)	11.1 (9.4–12.3)	8.7 (7.3–9.8)
DOM (%)	65 (61–68)	66 (63–72)	67 (64–71)	65 (62–67)
ADG (kg/day)	1.2	1.6	1.2	1.0

Crude protein (CP) and digestible organic matter (DOM) measured from cattle fecal samples, shown as mean (minimum–maximum), are determined over the phenologically-based predicted grazing window for each study year. See Figures 2, S4 and S6 for temporal patterns in crude protein and total digestible nutrients.

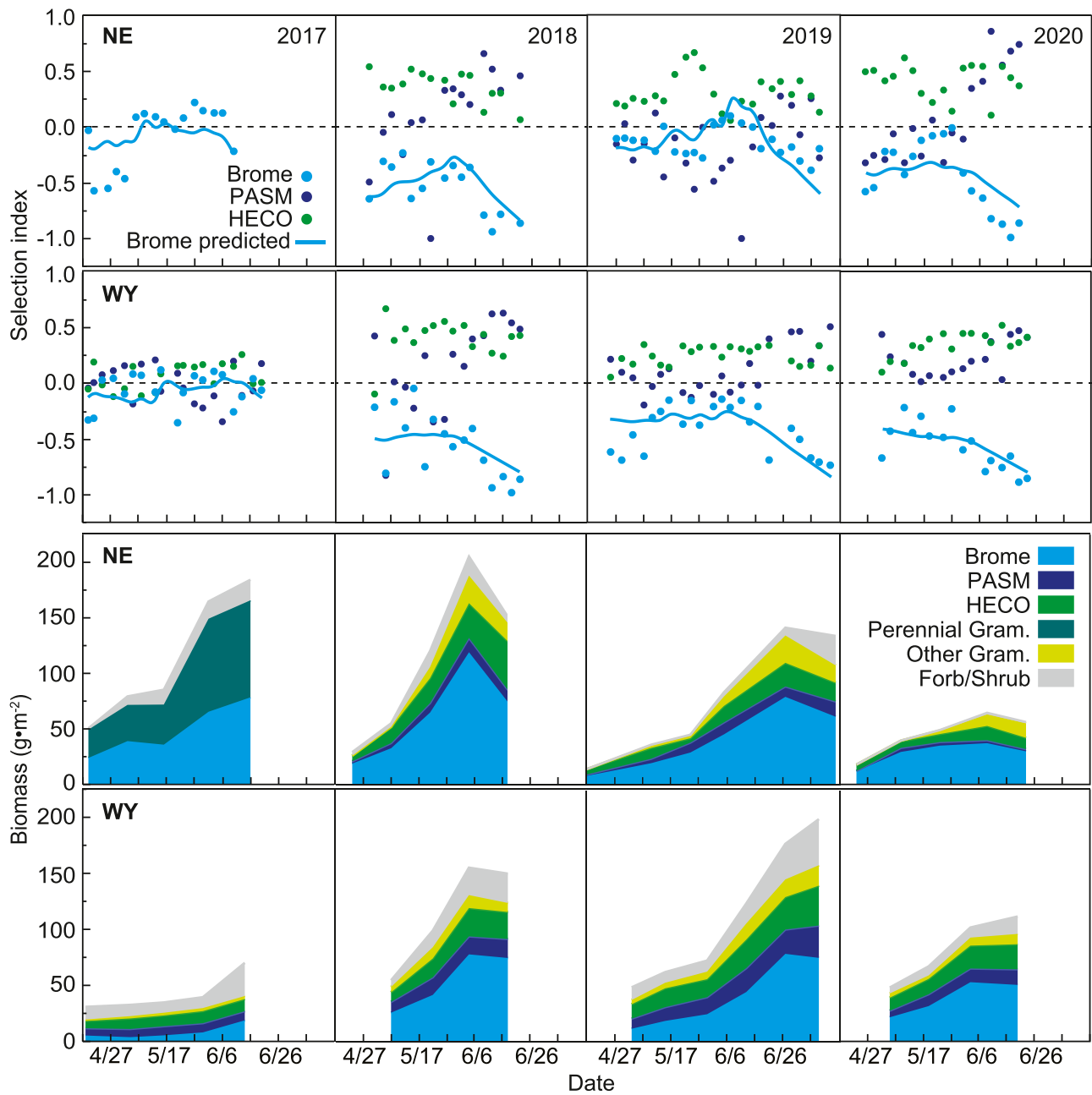
temperature and cumulative precipitation at each site for the 60 days preceding the mean date of the phenological stage of interest. Although the limited number of years within the study precluded robust analysis, warmer temperatures accelerated phenology (Fig. S5). Bromes reached 9.3 cm height earlier, brome height was greater at the time of flowering, and brome seeds matured earlier under warmer conditions. Seeds also matured earlier under drier conditions.

#### Grazing effects on brome seed production, cattle diet quality, and weight gains

Spring grazing reduced brome seed production by 30–77% relative to summer grazing (June–October) (Fig. 6). The largest reductions occurred during years with high brome production and consumption (2017, 2019), as well as in the final year at the WY site, despite lower rates of brome production and consumption (Figs. 1 and 4). Cattle weight gains and diet quality (measured at the WY site) remained relatively high and consistent across years during targeted grazing periods (Table 2).

#### Discussion

Phenological niche separation between invasive and native plant species often facilitates invasion, but it can also present op-



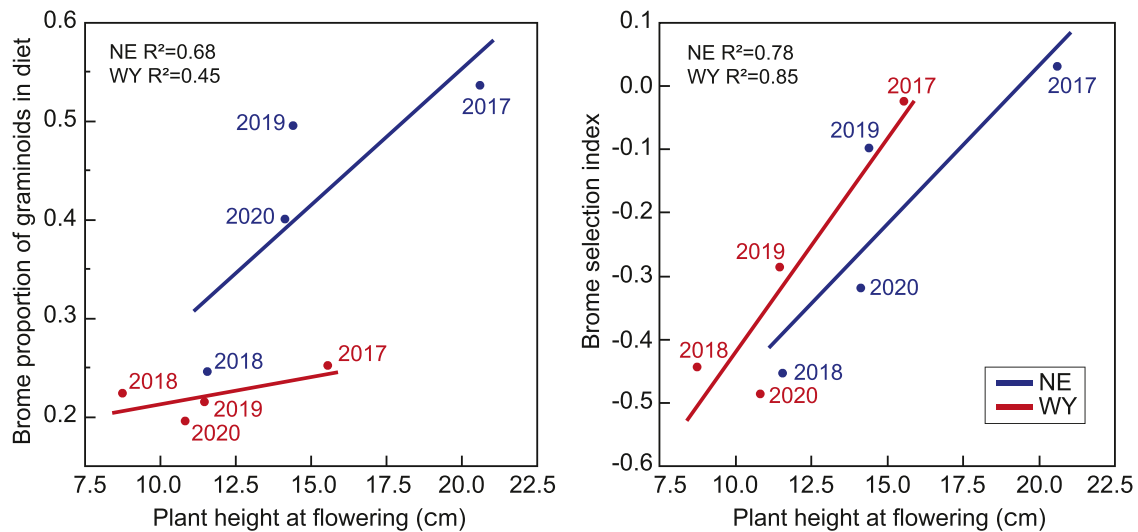
**Figure 4.** Observed and predicted cattle selection for annual bromes, and observed selection for dominant graminoid species (*P. smithii*, PASM, and *H. comata*, HECO) (upper panels), and biomass of dominant species and functional groups (including all sub-dominant perennial graminoids, other annual graminoids, and forb/shrub species) (lower panels). Predictions were generated for each date (month/day) on which diet composition was measured. Prediction lines are minimally smoothed splines that pass through the predicted data points (not shown). Values range from -1 (total avoidance) to 1 (total selection), with the dotted line indicating no selection. Because biomass was measured less frequently than consumption, interpolated biomass values were used to calculate selection index. In 2017 at the NE site, non-brome species were only sorted to functional group, precluding presentation of selection indices and biomass by species.

opportunities to implement carefully timed management (Wolkovich and Cleland 2011; Bennett et al. 2019; Hendrickson et al. 2020). Early season targeted grazing could exploit the advanced phenology of annual bromes relative to grazing-adapted native perennial plants in the western Great Plains, but it requires a better understanding of how phenology relates to livestock selection (Bailey et al. 2019). We found that two easy-to-measure phenological indicators, plant height and days after seed maturation, effectively predicted within-year patterns of cattle consumption and selection for annual bromes. A third metric, plant height at flowering, predicted which years hold the greatest potential for total brome consumption. Furthermore, spring grazing reduced annual

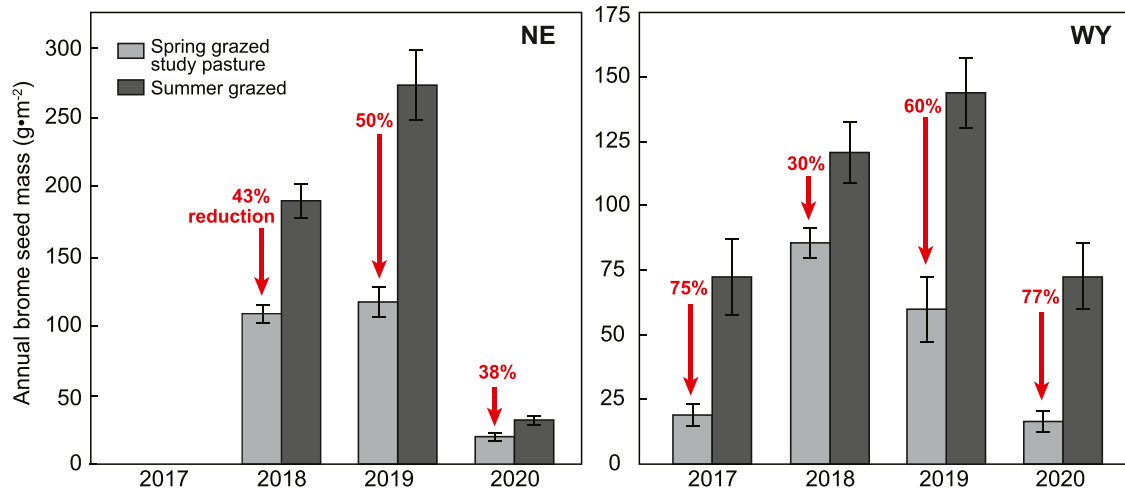
brome seed production by 30–77% relative to summer grazing in the surrounding pasture, and heifer weight gains were comparable to those previously observed at the WY site during the spring (Hart et al. 1988). These results indicate potential for appropriately timed targeted grazing to simultaneously control annual bromes and contribute to livestock production.

Changes in plant phenology reflect changes in both the accessibility and quality of annual bromes as forage. Annual brome height appeared to limit early season consumption, likely because short plants were difficult for cattle to access. Cattle consumption of annual bromes peaked when brome plants were tall but not yet mature (Fig. 1), corresponding to periods of high crude pro-





**Figure 5.** Season average brome consumption (left) and brome selection index (right), versus average plant height at flowering for the common sampling period across sites and years (12 dates between 5 May and 12 June).



**Figure 6.** Annual brome seed mass with targeted spring grazing and summer grazing in NE and WY, 2017–2020. Numbers above each pair of bars indicate the percent reduction in seed mass for spring grazing relative to summer grazing. Seed production was not measured at the NE site in 2017.

tein and energy content (Fig. 2, Fig. S4). Crude protein content declined linearly as bromes matured, falling below the level required for energy-efficient digestion (7%; Mathis and Sawyer, 2007) at approximately the same time that seeds matured. Seed maturation defined the end of the consumption period, likely because mature plants were both lower in forage quality and exhibited grazing avoidance traits, including stiff awns (Mosley and Roselle 2006). The fact that forage quality parameters were not the best predictors of brome consumption and selection (Table 1) suggests the importance of physical structures (e.g., awns) or other unexplained factors that contribute to reducing the palatability of annual bromes as seeds mature. Selection for annual bromes over native forage species, while relatively weak overall, was strongest during the period of peak brome consumption (Fig. 4). As annual bromes matured, cattle increasingly selected for relatively palatable native perennial grasses (Fig. S6) (Schwartz and Ellis 1981; Hodgson et al. 1994; Nelson and Moser 1994; Bailey 1995; Ganskopp and Bohnert 2009).

Using the phenological indicators height and days after seed maturation, we can define a grazing window for annual bromes to guide producers implementing early season targeted grazing in

this region (Figs. 1 and 3). Modeled grazing windows for these two mixed-grass prairie sites suggested that cattle will consume the most brome relative to native cool-season perennials when bromes are  $\geq 9.3$  cm tall and less than 1 day after seed maturation. During the four years studied, these predicted grazing windows lasted 35 d on average in NE, between 4 May and 8 June, and 42 d in WY, between 5 May and 16 June. At both sites grazing window duration varied widely among years because the beginning and end dates of windows did not change in concert. This variability suggests that controlling annual bromes through targeted spring grazing will require flexibility from producers in both timing and duration.

Our results suggest that targeted spring grazing can substantially increase cattle consumption of annual bromes relative to season-long grazing commonly used in the western Great Plains. Consumption of and selection for annual bromes both decline sharply as plants mature, with little consumption after seeds mature (Fig. 1B). The typical season-long grazing period (June–September) only overlaps with 12 of the 38 d of the average brome grazing window at our study sites, after which cattle would primarily select for native perennial species over annual bromes

where both are present. Season-long grazing may still inhibit annual bromes relative to no grazing (Porensky et al. 2020) as it involves some consumption of annual bromes and may select for invasion-resistant plant communities (Blumenthal et al. 2012). However, targeted spring grazing during annual brome grazing windows should maximize consumption of brome relative to native perennial grass species, greatly enhancing the ability of cattle to control bromes.

Across years, cattle selected for and consumed more annual bromes when average height was greater at the time bromes began flowering (Fig. 5). This metric provides a proxy for average yearly brome availability to cattle by indicating the length of time that brome is both tall and high in quality. These simple relationships explained 45–68% of the variation in brome consumption and 78–85% of variation in brome selection. They provide a rule of thumb to help producers implement spring targeted grazing, indicating that it is likely to be most effective in years when environmental conditions allow plants to grow taller before flowering. During our study, we did not observe years with substantial fall brome growth, which could lead to taller bromes the following spring (Mack and Pyke 1983) and potentially greater effectiveness of spring targeted grazing. In areas or years with sufficient fall brome growth, fall targeted grazing can also be effective (Schmelzer et al. 2014; Davies et al. 2021a; Vermeire et al. 2023).

The ability to predict optimal targeted grazing windows within and among years relied on accurate measurements of consumption of annual bromes over time. Dietary selection can be measured from bite count observations or inferred from monitoring animal location and grazing activity via GPS collars (Soder et al. 2009; Augustine and Derner 2013; Stephenson and Bailey 2017), but it remains challenging to quantify consumption of individual species in heterogeneous plant communities. Here, plant DNA from cattle fecal samples provided a time-integrated indicator of plant species contributions to cattle diets. However, this method has its limitations. In the present study, several dicots (forbs and shrubs) appeared to be over-represented in cattle diets given their rarity in our study pastures, which is consistent with prior studies using fecal DNA (King and Schoenecker 2019; Scasta et al. 2019). Consequently, we focused our analyses on graminoid consumption. Graminoids typically constitute > 70% of cattle diets in this region (Schwartz and Ellis 1981; Scasta et al. 2016). Despite these uncertainties, fecal DNA metabarcoding appears to work well for understanding temporal changes in consumption of a particular species, and may be broadly useful for precisely targeting the grazing of invasive species.

Cattle selection for annual bromes was greatest during our spring grazing window, but was generally lower than selection for native cool-season perennial grasses. Despite overall selection against bromes, however, maximizing brome selection with targeted spring grazing (Fig. 4) may be sufficient to reduce brome abundance. Compared with traditional summer grazing in adjacent pastures where most of the grazing pressure occurs after bromes have reached maturity, spring targeted grazing was associated with a reduction in brome seed production by 30–77% in our study pastures (Fig. 6). This result supports previous work suggesting that targeted grazing has the potential to reduce brome populations (Harmony 2007; Diamond et al. 2012; Davies et al. 2021a). Brome seed production and seed bank densities also declined after spring targeted cattle grazing in a mixed-grass prairie in Kansas, although brome populations recovered rapidly following the cessation of grazing treatments (Harmony 2007). Together, these studies demonstrate that targeted grazing can reduce annual brome fitness, but repeated targeted grazing in consecutive years will be necessary to effectively manage brome populations (Chambers et al. 2016; Sebastian et al. 2017). Consequently, spring grazing for annual bromes should be integrated into long-term grazing man-

agement. A key unanswered question is what level of brome consumption and resulting decrease in seed production is necessary to effectively suppress annual brome populations and restore native species.

It is important to note that our predicted grazing windows and observed effects of targeted grazing may be specific to western Great Plains rangelands where annual bromes coexist with native perennial grasses. In other regions, results of early spring targeted grazing have been mixed. Targeted cattle grazing reduced annual brome seed bank densities in Nevada uplands (Diamond et al. 2012; Schmelzer et al. 2014), but targeted sheep grazing had little effect on annual brome seed production in Montana sagebrush steppe (Lehnhoff et al. 2019). Fall and winter grazing has also shown promise for reducing litter and annual brome establishment in sagebrush steppe in Nevada and Oregon (Schmelzer et al. 2014; Perryman et al. 2020; Davies et al. 2021a). However, in the Intermountain West, native plant species have greater phenological overlap with annual bromes, and plant communities can be more sensitive to grazing (Mack and Thompson 1982; Milchunas et al. 1988; Loeser et al. 2007; Reisner et al. 2013; Williamson et al. 2020; Davies et al. 2021b, but see Copeland et al. 2021; Jordan et al. 2022). Therefore, it may be more difficult to alter the balance of competition in favor of native plants with targeted grazing. For both regions, longer term studies are needed to assess effectiveness of targeted grazing.

One potential limitation of early season grazing in the western Great Plains is that it could negatively affect native cool-season graminoids. In this study, cattle did often select for *H. comata* and *P. smithii* (Fig. 4). A key question is to what degree direct effects of grazing on cool-season graminoids are offset by reduced competition with annual bromes. Due to their longer growing season, native graminoids should be well positioned to use resources made available by reductions in brome populations. In a related study, native grass abundance increased with early season targeted grazing of introduced *Poa pratensis* L. (Kentucky bluegrass) and *Bromus inermis* (smooth brome) (Hendrickson et al. 2020). Determining the net effect of early season grazing on native cool-season species is a priority for future study, as producers consider implementing this annual brome management strategy.

Another promising avenue for future research is the potential for predicting brome phenology, and therefore consumption, from weather patterns. Annual brome growth is highly responsive to weather (Mack and Pyke 1983, 1984; Chambers et al. 2007; Bradley et al. 2016), which will influence brome phenology, and therefore selection of appropriate grazing windows. In the four years of our study, annual brome seed matured earlier under warmer, drier conditions, and height at flowering was generally greater in years with warmer springs (Fig. S5). With longer-term datasets, it may become possible to link annual brome phenological stages to climate data and predict the timing and efficacy of targeted grazing directly from climate conditions (e.g., Hartman et al. 2020; Gerst et al. 2021; Prev y et al. *in press*). However, even in the absence of such climate-phenology predictions, the easily observable phenological metrics identified here should be sufficient to guide grazing management decisions, both within and across years.

### Implications

Our results demonstrate that cattle consume annual bromes during a limited, predictable period in the early spring, and that grazing during this window may be an effective phenologically-based strategy for controlling annual brome invasion in the North American Great Plains. The cattle weight gains observed in our study further suggest that targeted spring grazing may simultaneously contribute to cattle productivity. Challenges will remain for

producers, such as targeting annual brome patches within large pastures, limiting cattle exposure to early season toxic plants (e.g., *Delphinium geyeri*, larkspur), and minimizing any negative effects on non-target early season species. These challenges may be addressed by technologies such as virtual fencing and precision herbicide application, together with periodic monitoring of plant community responses.

Spring targeted grazing may also prove useful in adapting annual brome management to climate change. In mixed-grass prairie, experimental warming has been found to expand *B. tectorum*'s phenological niche and increase invasion (Blumenthal et al. 2016). Taking advantage of warmer spring temperatures to shift to an earlier grazing season may help counteract such changes. Under both current and predicted future climatic conditions, the keys to successful targeted grazing will be to maintain flexibility in response to variation in annual brome height and seed maturation time within and across years, and to deplete the seed bank with repeated targeted grazing treatments.

More generally, our results show that combining temporal analyses of livestock diets and plant phenology can be useful for precisely targeting grazing of invasive species. This approach holds promise for improving management of a wide array of invasive plants. Where successful, such precision targeted grazing may benefit native biodiversity while sustaining livestock production across millions of hectares of rangeland.

#### Declaration of Competing Interest

The authors declare no conflicts of interest.

#### CRediT authorship contribution statement

**Julie A. Kray:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing – original draft, Writing – review & editing. **Dana M. Blumenthal:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Mitchell B. Stephenson:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Lauren M. Porensky:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Validation, Visualization, Writing – original draft, Writing – review & editing. **David J. Augustine:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Validation, Visualization, Writing – original draft, Writing – review & editing. **Seth J. Romero:** Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Writing – original draft, Writing – review & editing. **Matt C. Mortenson:** Data curation, Investigation, Methodology, Project administration, Resources, Writing – original draft. **Justin D. Derner:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

#### Data Statement

Data from this study are available in Dryad: [doi:10.5061/dryad.wdbrv15z5](https://doi.org/10.5061/dryad.wdbrv15z5).

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#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.rama.2024.08.024](https://doi.org/10.1016/j.rama.2024.08.024).

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