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Variation in sage-grouse habitat quality metrics across a gradient of feral horse use

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ABSTRACT

Feral horse (*Equus ferus caballus*) grazing can alter arid shrubland habitat in the western United States to the detriment of sympatric wildlife species, including the greater sage-grouse (*Centrocercus urophasianus*). To date, studies of horse-influenced habitat alteration have only occurred in a few locations and have infrequently represented gradients of horse use. We investigated whether greater sage-grouse habitat quality metrics were negatively associated with feral horse use in southcentral Wyoming, USA. We also tested whether utilization distributions generated from feral horses tracked with global position system transmitters were correlated with dung pile density, our index of horse use. Dung pile density did not vary among utilization distribution levels, indicating utilization distributions were a poor predictor of cumulative horse use. Bare ground increased with dung pile density ($\beta = 0.06$, 85% CI = 0.04–0.18), and grass height exhibited a threshold response and began to decline after 638 piles/ha. Other habitat metrics including percent shrub cover, native perennial grass cover, and visual obstruction were better explained by topographic and temporal variation. Our results suggest that herd size reduction may limit soil erosion potential and improve desired herbaceous structure, though additional management actions regarding feral horse use are needed to sustain high-quality greater sage-grouse habitat.

1. Introduction

After the extinction of most Pleistocene megafauna, arid western North American shrublands evolved under warmer and drier climates with relatively lower grazing pressure compared to grasslands and savannahs (i.e., the American Great Plains; Mack and Thompson, 1982). American bison (*Bison bison*) were still widely distributed across western North America after the Pleistocene but were frequently absent within large geographic areas for extended time periods likely due to spatio-temporal variability in resources and hunting pressure from Native Americans (Bailey, 2016). Consequently, the graminoid species in the understory of arid shrublands are more sensitive to repeated herbivory by large introduced grazers, feral horses (*Equus ferus caballus*) and cattle (*Bos taurus*; Mack and Thompson, 1982). Mismanagement of both feral horse and cattle grazing can negatively affect arid shrubland ecosystems (e.g., Kauffman et al., 1983; Batchelor et al., 2015; Davies and Boyd 2019), necessitating informed and careful decision-making when managing either species. While livestock on public rangelands in the United States are managed under a federal permitting system to optimize the timing, intensity, and duration of use to maintain ecosystem functions, horse grazing management is less structured. In part, it is the Wild Free-Roaming Horses and Burros Act (Public Law 92–195, 1971) that prevents the application of an analogously managed grazing structure for feral horses, leading to largely unrestricted horse grazing. This translates into a greater potential for feral horses to negatively influence arid shrublands, a current concern considering recent escalation in their abundance (Bureau of Land Management, 2020). Limited funds (Garrott and Oli, 2013) and legislative impediments (Scasta et al., 2018) have in part led to the dramatic increase in population sizes of feral horses on Bureau of Land Management land, with recent estimates of 79,568 individuals (Bureau of Land Management, 2020). This is >300% of the maximum appropriate management level, a population limit set to maintain a thriving natural ecological balance (Public Law 95–514, 1978).

Feral horses alter shrubland structure and composition through consumption, trampling, and as vectors of invasive species spread (Beever and Aldridge, 2011; King et al., 2019). Horse-grazed sites, compared to areas where horses have been removed or excluded, exhibit undesirable rangeland characteristics including lower vegetation biomass and greater soil penetration resistance (Beever et al., 2008;

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Davies et al., 2014). Mesic areas receive proportionally greater use from feral horses (Crane et al., 1997) and grazing effects in riparian or riparian-adjacent areas have been well-studied (e.g., Beever and Brussard 2000; Boyd et al., 2017). How more xeric upland sites respond to horse use is comparatively understudied; yet, answering this question is critical considering the potential indirect effects on sympatric wildlife (Beever and Aldridge, 2011; Davies et al., 2014).

The greater sage-grouse (*Centrocercus urophasianus*; henceforth 'sage-grouse') is a species particularly vulnerable to shrubland habitat alteration (Beck et al., 2012). Habitat loss and alteration and concomitant declining populations have led to greater sage-grouse being petitioned eight times for protection under the Endangered Species Act of 1973 (Public Law 93–205, 1973; U.S. Fish and Wildlife Service, 2010, 2015). Consequently, sage-grouse are the focus of several broad-scale management efforts to conserve its habitat quality (e.g. Chambers et al., 2017). Approximately 12% of current sage-grouse range overlaps with areas managed for feral equids, and this overlap can result in decreased nesting and escape cover, and/or reduced forage availability for sage-grouse (Beever and Aldridge, 2011). Consequently, feral equid grazing is considered a threat to several sage-grouse populations (U.S. Fish and Wildlife Service, 2013).

Research on horse-induced habitat alteration has mainly focused on differences between grazed and un-grazed sites (e.g., Baur et al., 2017; Beever et al., 2008; Fahnestock and Detling, 1999; Freedman et al., 2011; Lopez et al., 2017). These experiments have proved invaluable for revealing the negative effects of horse occupation on rangelands. Even so, grazing is not a binary disturbance and is more realistically quantified as a continuous variable such that heavily used areas may exhibit a greater degree of alteration than areas with lighter use, and this relationship may be non-linear (Davies and Boyd, 2020). Currently, removal gathers (or musters) are the primary tool for managing horse populations in the United States; but these temporary reductions in herd size do not restrict when or where horses may graze. Without restricting horse access to some areas (i.e., exclosures), there may be little variation in habitat quality metrics due to relatively even grazing pressure across the landscape, particularly if horses exceed the appropriate management level.

We designed our study to evaluate variation in sage-grouse habitat quality metrics across a gradient of feral horse use within the Red Desert of southcentral Wyoming, USA. We identified 8 metrics known to influence habitat quality for sage-grouse (Table 1) and examined the response of these metrics to an index of feral horse use. We also assessed the potential for utilization distributions to be used as an adequate index of total horse population use. We expected percent shrub cover, shrub height, perennial grass cover, grass height, and visual obstruction to decrease, but shrub fragmentation, bare ground, and cheatgrass (*Bromus tectorum* L.) cover to increase with greater horse use.

2. Material and methods

2.1. Study area

We conducted our study within the Adobe Town Herd Management Area located in southern Wyoming, USA (Fig. 1). The management area covers 3413 km^2 and is classified as cold-arid-steppe (Kottek et al., 2006) with elevation ranging from 1883 to 2506 m (USGS 2016a) and annual mean 30-year normal precipitation and temperatures of 27.7 cm and 6.0 °C, respectively (PRISM Climate Group 2020). Dominant shrub species included Wyoming big sagebrush (*Artemisia tridentata* Nutt. *Wyomingensis* Beetle & Young), greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.), yellow rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), rubber rabbitbrush (*Ericameria nauseosa* (Pall. ex Pursch) G.L. Nesom & Baird), and assorted saltbush species (*Atriplex* spp.). Perennial grass species included cool-season (C3 photosynthetic pathway) bunchgrasses such as squirreltail (*Elymus elymoides* (Raf.) Swezey), prairie Junegrass (*Koeleria macrantha* (Ledeb.) Schult.), and Sandberg's bluegrass (*Poa secunda* J. Presl), along with warm-season (C4 photosynthetic pathway) grasses such as inland saltgrass (*Distichlis spicata* (L.) Greene), and sandhill muhly (*Muhlenbergia pungens* Thurb.). Cheatgrass was the main exotic annual grass present. Estimated herd size was within appropriate management level (610–800 horses) in 2018 but was 24% above appropriate management level in 2019, the years of our study (Bureau of Land Management, 2020). Our study area included six livestock allotments permitted for summer grazing by cattle (*Bos taurus*). Allotted animal unit months between March and November totaled 6596. The study area provided crucial habitat for iconic wildlife species including sage-grouse, elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*).

Table 1
The set of sagebrush habitat quality metrics measured across a gradient of feral horse (*Equus ferus caballus*) use, along with their importance to greater sage-grouse (*Centrocercus urophasianus*) and predicted response of each metric from increased horse use, Adobe Town Herd Management Area, Wyoming, USA, June through August 2018–2019.

Habitat quality metric	Importance to sage-grouse	Predicted response	Justification citation
Bare ground[a]	Indirect effects on habitat quality	Increase	Davies and Boyd (2019)
Shrub cover[a]	Food resource; yearlong habitat	Decrease	Crawford et al. (2004)
Shrub height[b]	Nesting habitat	Decrease	Connelly et al. (2000)
Shrub fragmentation[c]	Escape cover, nest concealment	Increase	Schroeder and Baydack (2001)
Native perennial grass cover[a]	Escape cover, nest concealment	Decrease	Aldridge and Boyce (2007)
Cheatgrass cover[a]	Indirect effects on habitat quality	Increase	(Connelly et al., 2004)
Grass height[d]	Nest and brood concealment	Decrease	Doherty et al. (2014)
Visual obstruction[e]	Nest and brood concealment	Decrease	Doherty et al. (2010)

[a] Mean percent canopy cover.
[b] Mean sagebrush height.
[c] Maximum length of shrub intercepts (Beever et al., 2008).
[d] Mean droop height.
[e] Mean Robel pole reading.

2.2. Horse use and field data collection

We used location data from horses equipped with global positioning system (GPS) transmitters to generate vegetation and soil sampling locations within the study area. As part of a concurrent research project, we attached Lotek Wireless IridiumTrackM 3D GPS (Lotek Wireless, Inc., Newmarket, Ontario, Canada) or Vectronic Vertex Lite GPS (Vectronic Aerospace GmbH, Berlin, Germany) collars to adult (>4 years of age) female horses in 2017. All collars included 2-way Iridium-based satellite communication and recorded location fixes every 2 h. All animal handling and use followed protocols approved by the Institutional Animal Care and Use Committee of the University of Wyoming (protocol #20160826DS00249) and were applied within the criteria set forth in the DOI-BLM-WY_DO30_0104-EA Environmental Assessment (Bureau of Land Management, 2016).

Using horse location data beginning on 1 May each year, we constructed utilization distributions for horse groups (bands) containing a GPS-collared individual using dynamic Brownian Bridge movement models (Kranstauber et al., 2012). Horses form static social groups and therefore the locations of one individual reflect locations of the entire group. During the 2018 data collection period, 18 unique horse bands featured a collared individual compared to 15 bands in 2019. We divided each utilization distribution into strata based on levels of predicted use: high (top 10% of use), moderately high (>10–25%), moderately low (>25–50%), and low (>50%). For each horse by stratum

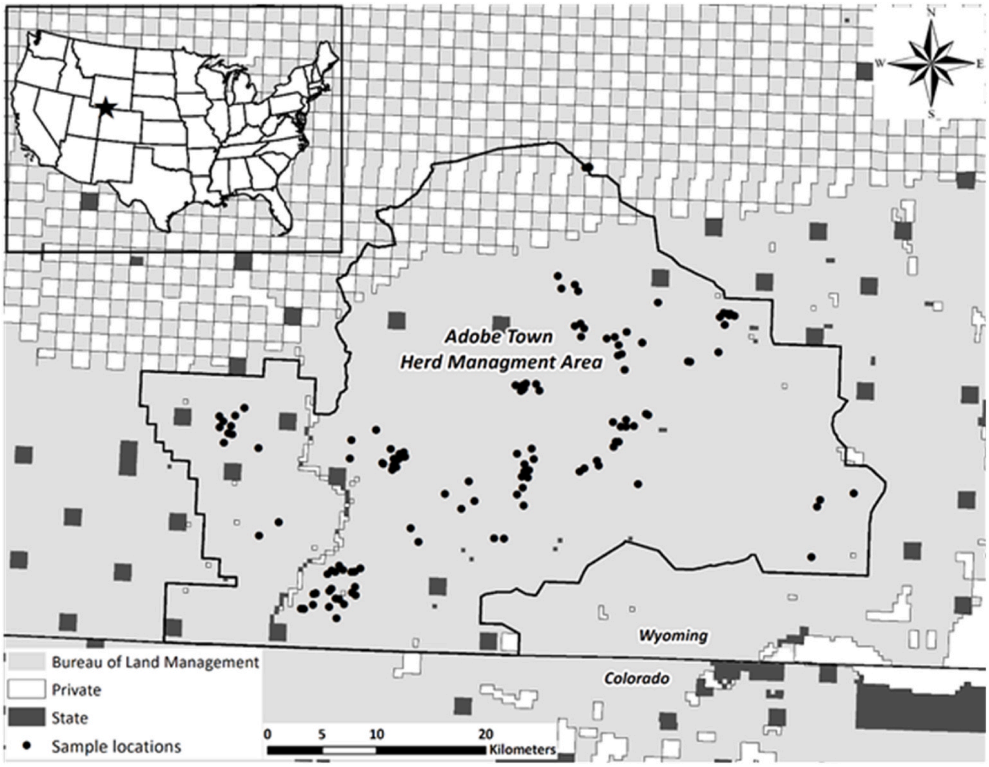

Fig. 1. Sample locations and land surface ownership within the Adobe Town Herd Management Area in south-central Wyoming, USA, June through August 2018–2019.

combination, we randomly selected a sample location used by the horse within the previous 2 weeks. We constrained sampling availability to sagebrush habitat defined by LANDFIRE Existing Vegetation Type 1.4 (USGS 2016b) and aimed to lessen topographic influence by constraining sample sites to fall within one standard deviation of the mean slope, elevation, and compound topographic index of the study area. After completing one round of field data collection, we updated utilization distributions with newly acquired location data and repeated the sample selection process. We ensured that samples were evenly distributed across each horse band by utilization distribution combination by sampling one location per utilization distribution level per band per year.

At each sample location we measured variables known to influence habitat quality for sage-grouse (Table 1). To quantify vegetation structure and composition at each sampling location, we established four perpendicular 50-m transects oriented along each cardinal direction. We measured percent shrub canopy cover and gap length between shrubs using the line-intercept method (Canfield 1941). We assessed sagebrush height by measuring the maximum height of the plant at the center location and along each transect at 5, 15, 25, 35, and 45 m intervals ($n = 21$). We recorded visual obstruction readings using a Robel pole (Robel et al., 1970) and quantified vegetation composition using 0.5 m^2 (100 cm × 50 cm) Daubenmire quadrats (Daubenmire, 1959) at the same intervals. Within each Daubenmire quadrat we estimated canopy cover of the following 13 plant functional groups and ground cover classes: cheatgrass, native annual grasses, native perennial C3 grasses, and native perennial C4 grasses, sedges, forbs, cacti, shrubs, litter, bare ground, lichen, biological soil crust, and rocks; via the following cover classes: 0, <1%, 1–5%, 6–25%, 51–75%, 76–95%, >96% (Scasta et al., 2016). To increase estimation accuracy, we taped sections of the quadrat to signify polygons representing 5% and 25% of the quadrat area. We recorded the droop height of the tallest grass specimen present within the 5% polygon to assess grass height (Connelly et al., 2004).

Ungulate fecal counts can be a useful metric for intensity of use and is relatively easy for managers and researchers to employ (Forsyth et al., 2007). To determine if utilization distribution levels were a similarly effective predictor of horse use, we counted individual fecal piles for horses within 2 m along both sides of each of the four, 50-m perpendicular transects (800 m^2; Beever and Brussard 2004). Male horses defecate in latrines, which make counting these piles difficult; thus, we did not include such piles in our counts (Street 2020). To account for use by cattle and wild ungulates (elk, mule deer, and pronghorn), we counted fecal piles for these species as well. Species-specific identification of native ungulate feces was difficult to universally apply, therefore counts for these native ungulates were pooled together and analyzed collectively.

2.3. *Spatial data*

We identified topographic, soil, and precipitation variables that could explain variation among shrubland habitat metrics. We used ArcGIS Geomorphometry & Gradient Metrics toolbox (Evans et al., 2014) within ArcMap 10.6.1 (ESRI, 2018) to create 30-m rasters of aspect, compound topographic index, and slope from a digital elevation model (DEM; USGS 2016a). We used POLARIS Soil Properties (Chaney et al., 2019) to create 30-m rasters of mean percent sand, silt, and clay at both 0–5 cm, and 5–15 cm depths. We used daily 4-km precipitation data (PRISM Climate Group 2020) to obtain estimated precipitation at each sample location for the 14 days prior to sample date.

2.4. *Statistical analyses*

We conducted a one-way analysis of variance test with Tukey's honestly significant difference adjustments (Tukey 1953) to determine whether mean fecal pile density was significantly different across the 4 utilization levels at the $\alpha = 0.05$ level. We then compared which horse use metric, utilization level or fecal pile density, better fit each habitat variable using linear models. We ranked models using Akaike's

Information Criterion corrected for small sample sizes (AIC_c; (Burnham and Anderson, 2002)) and used the top ranked variable as our metric of horse use in the following analyses.

We performed a multi-stage model selection process using the “spdep” (Bivand et al., 2013) and “spatialreg” (Bivand and Piras, 2015) packages within program R (R Core Team, 2019). We first assessed which abiotic, biotic, and temporal variables were informative predictors of each habitat metric. To do this, we generated linear models for all combinations within each of the following categories: topographic, temporal, soil texture, ungulate use, and precipitation variables (five model sets). We also examined whether a linear or quadratic term for horse use best fit each response variable. We used AIC_c to rank models within each set and calculated model-averaged 85% confidence intervals for variables found in models <2 AIC_c of the top model to assess informative predictors (Arnold, 2010). For models not meeting assumptions of normality or homoscedasticity, we applied an arcsine transformation to response proportion variables (native perennial grass and cheatgrass cover) and a square root transformation to non-proportion variables (visual obstruction). Informative predictors from each model set were brought forward into a final model set. All soil texture variables were highly correlated ($r > 0.95$), therefore only one variable was included per model and only the top ranked variable, if it was informative, was brought forward.

We then generated linear models using all variable combinations within the final model set for each habitat variable. We calculated a Moran’s I statistic (Moran, 1948) to assess if model residuals were significantly spatially dependent at the $\alpha = 0.05$ level. If spatial dependency was present, we first added location coordinates as model covariates; however, if that did not adequately account for spatial autocorrelation we assessed Lagrange Multiplier test diagnostics (Anselin, 1998) to determine whether a spatial lag or spatial error model was most appropriate to employ. If applicable, we re-ran models using the appropriate spatial regression model and confirmed final models were not spatially autocorrelated (Moran’s I) and conformed to homoscedasticity assumptions (Breusch-Pagan test; Breusch and Pagan 1979). We ranked all models using AIC_c and present model-averaged parameter estimates, standard errors, and 85% confidence intervals for all variables found within models <2 AIC_c of the top ranked model (Arnold, 2010).

3. Results

We measured habitat variables at 131 locations between June and August in 2018 ($n = 72$) and 2019 ($n = 59$). The number of horse fecal piles per sample location ranged from 150 to 1462 per ha ($\bar{x} = 504.3$, SD = 228.2). The number of cow pats ranged from 0 to 888 per ha ($\bar{x} = 100.6$, SD = 144.6) and were uncorrelated with horse fecal piles ($r = -0.01$, $P = 0.89$). Native ungulate fecal piles ranged from 63 to 2100 per ha ($\bar{x} = 547.5$, SD = 363.5) and were negatively correlated with horse fecal piles ($r = -0.09$, $P = 0.09$). Mean number of horse fecal piles decreased from the highest to lowest utilization levels, but analysis of variance results revealed no difference among group means ($F_{3,127} = 1.86$, $P = 0.14$; Fig. 2). Between the metrics of horse use, the number of fecal piles per location was a better fit for all response variables than the categorical variable of utilization levels; therefore, we used fecal piles as the metric of horse use for subsequent analyses.

Horse use appeared in highly ranked models explaining variation in percent bare ground and grass height (Table 2). Bare ground increased with horse use ($\beta = 0.11$, SE = 0.04; Fig. 3A) and as the summer progressed ($\beta = 0.16$, SE = 0.04), but declined with steeper slopes ($\beta = -1.40$, SE = 1.09) and higher elevations ($\beta = -0.05$, SE = 0.02; Table 3). A quadratic term of horse use explained grass height better than the linear term (Table 2). Grass height declined after approximately 638 horse fecal piles/ha (Fig. 3B) and was higher in 2019 than 2018 ($\beta = 2.07$, SE = 0.46; Table 3). Horse use was not informative for explaining

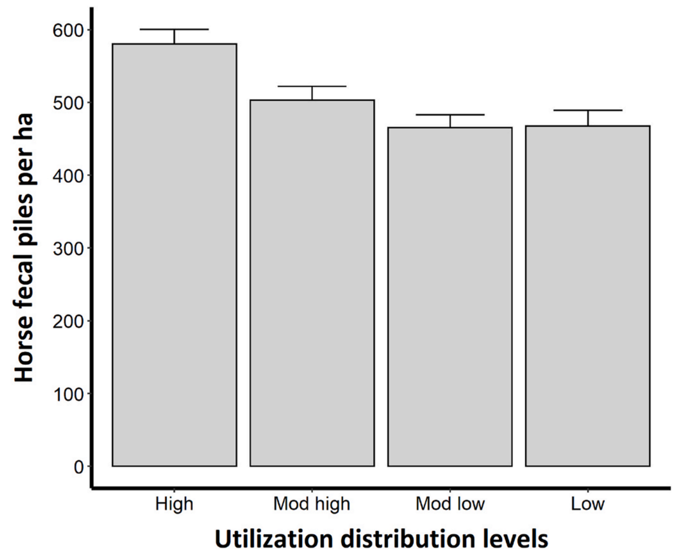

Fig. 2. Mean (SE) density of feral horse (*Equus ferus caballus*) fecal piles per utilization distribution level. Group means were not statistically different according to Tukey’s honestly significant difference adjustments ($F_{3,127} = 1.86$, P = 0.14).

variation in any other habitat metric (Table 3). Perennial grass cover was higher in 2019 than 2018 ($\beta = -0.03$, SE = 0.01) and increased with elevation ($\beta = 0.02$, SE = 0.01). Cheatgrass cover declined with both elevation ($\beta = -0.03$, SE = 0.01) and percent silt at the 5–15 cm depth ($\beta = -0.23$, SE = 0.04). Shrub height increased with percent sand at the 5–15 cm depth ($\beta = 0.12$, SE = 0.05), but declined with higher elevations ($\beta = -0.04$, SE = 0.02), and decreased with native ungulate use ($\beta = -0.10$, SE = 0.03). Maximum shrub intercept length was also negatively associated with native ungulate use ($\beta = -0.66$, SE = 0.19; Table 3). No measured variables were informative predictors of visual obstruction or shrub cover (Table 3).

4. Discussion

Our results add to the existing body of literature that demonstrate links between feral horse grazing and reduced environmental quality (Davies and Boyd, 2019; Eldridge et al., 2020). Specifically, we show that greater intensity of feral horse use may negatively influence soil health and undesirably alter herbaceous structure in xeric shrubland systems. Contrary to our predictions though, we found no support for horse use in explaining variation of other sage-grouse habitat quality metrics. Our study was strictly correlative and therefore we cannot infer causation; yet our work demonstrates that reducing herd sizes may improve certain aspects of sage-grouse habitat quality, but additional management actions regarding horse use are needed to maintain overall high-quality habitat.

The link between increased horse use and percent bare ground is troubling because a high proportion of bare ground is an indicator of poor soil quality and subsequently rangeland health (Derner et al., 2018; Pyke et al., 2002). Without protection from vegetation and litter, exposed areas of bare ground are prone to increased soil erosion and exotic plant invasion (Davies and Boyd, 2019). Increased runoff and sediment loss from erosion reduces water and nutrient availability for plant growth and propagation (Rostagno et al., 1991). This often leads to decreased vegetation production and may also result in unwanted state changes (Chartier and Rostagno, 2006; Pimentel et al., 1995). Though we did not find a link between horse use and cheatgrass cover, bare ground is highly susceptible to cheatgrass invasion (Jessop and Anderson, 2007). Cheatgrass establishment is a major threat to western US rangelands because it leads to decreased plant diversity, altered

Table 2
Candidate models for explaining variation in sagebrush habitat metrics across a gradient of feral horse (*Equus ferus caballus*) use within the Adobe Town Herd Management Area, Wyoming, USA, from June through August 2018–2019. Models <2 AIC_c of top model are shown, in addition to the null model.

Model	K	AIC_c	ΔAIC_c	w_i
Bare ground cover				
Horse + Elevation + Day + Slope	6	978.3	0.00	0.12
Horse + Elevation + Day + Slope + Ungulate	7	978.3	0.03	0.12
Horse + Elevation + Day + Slope + Silt[a]	7	978.8	0.54	0.09
Horse + Elevation + Day + Slope + Ungulate + Silt[a]	8	979.3	1.03	0.07
Horse + Elevation + Day + Silt[a]	6	979.3	1.04	0.07
Horse + Elevation + Day + Slope + Ungulate + Cattle	8	980.1	1.77	0.05
Horse + Elevation + Day	5	980.1	1.84	0.05
Null	3	1011.8	30.48	0.00
Native perennial grass cover				
Elevation + Day + Year + Ungulate	7	−318.4	0.00	0.33
Elevation + Day + Year + Ungulate + Cattle	8	−317.3	1.11	0.19
Null	3	−292.1	26.34	0.00
Cheatgrass cover				
Silt[a] + CTI + Elevation + Latitude + Longitude	7	−393.5	0.00	0.50
Silt[a] + CTI + Elevation + Aspect + Latitude + Longitude	8	−393.4	0.16	0.46
Null	5	−336.3	57.22	0.00
Grass height				
Aspect + Year + Latitude + Longitude	6	633.1	0.00	0.25
Year + Horse + Horse^2 + Latitude + Longitude	7	633.3	0.23	0.23
Year + Latitude + Longitude	5	633.5	0.37	0.21
Aspect + Year + Horse + Horse^2 + Latitude + Longitude	8	634.1	0.98	0.16
Null	4	646.3	13.17	0.00
Visual obstruction				
Ungulate	4	226.2	0.00	0.94
Null	3	231.8	5.53	0.06
Shrub cover				
Ungulate	3	−373.9	0.00	0.23
Ungulate + Aspect	4	−373.3	0.57	0.17
Ungulate + Cattle	4	−372.1	1.74	0.10
Ungulate + Horse	4	−372.0	1.87	0.09
Null	2	−371.6	2.26	0.07
Shrub height				
Elevation + Sand[a] + Ungulate	6	948.1	0.00	0.57
Null	3	969.8	21.73	0.00
Maximum shrub intercept length				
Ungulate	3	1459.1	0.00	0.32
Ungulate + Slope	4	1459.3	0.17	0.29
Ungulate + Year	4	1460.0	0.91	0.20
Ungulate + Slope + Year	5	1460.2	1.07	0.19
Null	2	1469.9	10.75	0.00

[a] 5–15 cm depth.

herbaceous structure, and increased fire frequency, all of which combine to reduce sage-grouse habitat quality (Connelly et al., 2004; Knapp, 1996, (Lockyer et al., 2015).

Separating the individual ecological effects of feral horses and cattle is notoriously difficult (Davies and Boyd, 2019). We attempted to account for additional use at each site from cattle and also native ungulates by using fecal counts as a metric of use and allowing these metrics to compete with horse use to explain variation in response variables. The fact that horse and cattle fecal counts were uncorrelated underscores the difficulty in disentangling the effects of both species as our results indicate inconsistent overlap in use by both species. The relationship between horse and native ungulate fecal counts may have implications for native ungulate habitat quality. We know that co-occurring animals alter their behavior at water sources in arid systems (Gooch et al., 2017; Osterman-Kelm et al., 2008; Perry et al., 2015), but it is unknown whether this extends to other areas. The weak, but negative, correlation between horse and ungulate fecal piles is an interesting result that elicits future investigation of potential niche partitioning among species or avoidance of higher horse use areas by native ungulates.

Differences in vegetation height between areas with and without feral horse grazing have been documented in several systems (Beever and Brussard, 2000; Boyd et al., 2017; Eldridge et al., 2019). Here we present a threshold response of grass height to a gradient of horse use. We detected this threshold response because the quadratic term for horse use was a better fit than the linear term. We acknowledge that grass height only minimally declined at greater use levels; nonetheless, this result has important implications to sage-grouse habitat quality as taller grass provides better nest concealment and cover for chicks (Beck and Mitchell, 2000; Doherty et al., 2014; Hagen et al., 2007; Holloran et al., 2005). It is critical to note that we measured grass height during summer following the nesting period for sage-grouse; thus, our results are only applicable to understanding the potential for horses to negatively influence brood-rearing habitat. Furthermore, advanced phenological expression of grasses during our sampling period ensured shorter grasses at sampling locations were not merely a factor of measuring them before they reached their potential height, which has led to spurious results in past models of sage-grouse nest success (Gibson et al., 2016; (Smith et al., 2018).

We attribute the responses of bare ground and grass height to differences in anatomy and use between horses and co-occurring ungulates. Unlike native ungulates and cattle, horses possess upper incisors (Janis, 1976). This adaptation assists horses in clipping vegetation closer to the ground than sympatric species, which can affect the ability for vegetation to regrow following herbivory (Menard et al., 2002; Symanski, 1994). While densities of pronghorn, the most common native ungulate in this area, are greater than for horses (WGFD, 2018; Bureau of Land Management, 2020), horses are much larger (~400 kg vs. ~50 kg; (Berger, 1986); Garland, 1983) and thus have greater capacity to compact soil, further hindering plant growth (Beever and Herrick, 2006; Kozlowski, 1999). Total mule deer abundance in the surrounding area is also greater than horse abundance (Wyoming Game and Fish Department, 2018), but many mule deer migrate out of the study area during the growing season (Kaufmann et al., 2020), limiting their effects. Estimates of elk in this region are missing mainly due to their high mobility (Wyoming Game and Fish Department, 2018); but they likely have lower densities than horses and thus less potential to influence habitat characteristics. Cattle are similar in size to horses, but they are only on-range for a limited period of time during the year, and their densities vary yearly in response to precipitation and range condition (Bureau of Land Management, 2016). Consequently, even in years where densities of horses and cattle are similar, there is more consistent grazing pressure from horses throughout the year, translating into greater potential for horses to negatively affect rangeland conditions.

Fecal piles have frequently been used as an index of relative ungulate use (Forsyth et al., 2007; Goda et al., 2008; Rhodes et al., 2017; Street 2020). Because we concurrently had GPS-collared horses with 2-way Iridium-based technology, we were able to assess the efficacy of near-real time horse data in assessing cumulative population use. Fecal piles did not significantly vary among the four utilization distribution levels and while this may seem surprising given the call for more fine-scale movement data to improve our understanding of habitat use (Cagnacci et al., 2010), there are several reasons why individual utilization distributions were uninformative in our experiment. First, 4–12 weeks of GPS data (336–1008 locations assuming a 2-h fix rate) may not be a sufficient sample size to properly estimate and differentiate between use levels. Second, we observed a wide range in the number of individuals per horse band (2–15, unpublished data) and many other bands without a collared individual. Fecal pile counts capture the increased use of larger bands of horses and horse bands without collared

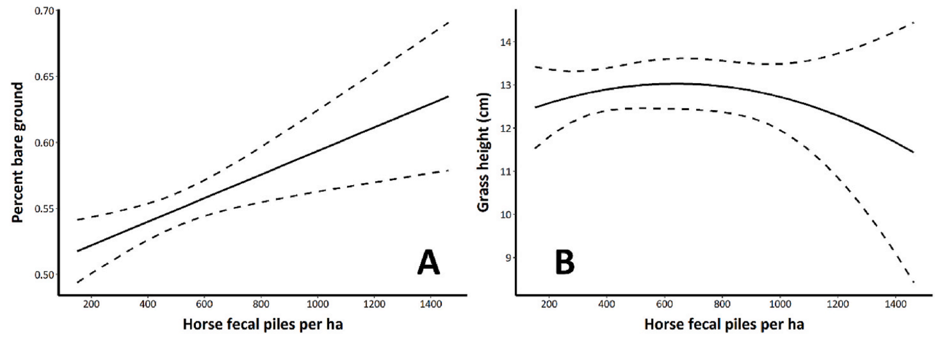

Fig. 3. Predicted values (85% CIs) of A) percent bare ground and B) mean grass height by number of feral horse (*Equus ferus caballus*) fecal piles per hectare, Adobe Town Herd Management Area, Wyoming, USA, June through August 2018–2019. Grass height began to decline at 638 fecal piles/ha.

Table 3
Model-averaged parameter estimates, standard errors, and 85% confidence intervals for informative variables explaining variation in sagebrush habitat metrics across a gradient of feral horse (*Equus ferus caballus*) use within the Adobe Town Herd Management Area, Wyoming, USA, from June through August 2018–2019.

Parameter	Estimate	SE	85% CIs
Bare ground			
Intercept	121.44	31.40	(76.39, 166.49)
Slope	−1.40	1.09	(-3.10, −4.47)
Day	0.16	0.04	(0.10, 0.22)
Horse	0.11	0.04	(0.04, 0.19)
Elevation	−0.05	0.02	(-0.07, −0.02)
Native perennial grass cover			
Intercept	−3.62	2.29	(-6.92, −0.33)
Rho [a]	0.39	0.10	(0.24, 0.54)
Year2019	−0.28	0.11	(-0.45, −0.12)
Exotic annual grass cover			
Intercept	8.51	1.59	(5.38, 11.64)
CTI	−0.07	0.03	(-0.12, −0.01)
Grass height			
Intercept	−48.75	29.95	(9.35, 13.26)
Year2019	1.85	0.48	(1.43, 2.77)
Horse	0.03	0.05	(0.02, 0.14)
$Horse^2$	−0.00	0.00	(-0.00, −0.00)
Visual obstruction			
Intercept	1.76	0.30	(1.33, 2.20)
Rho [a]	0.30	0.12	(0.12, 0.47)
Shrub cover			
Intercept	0.17	0.01	(0.15, 0.19)
Shrub height			
Intercept	117.79	35.82	(66.23, 169.35)
Rho [a]	0.21	0.13	(0.03, 0.39)
Sand [b]	0.12	0.05	(0.05, 0.19)
Ungulate	−0.10	0.03	(-0.15, −0.06)
Elevation	−0.04	0.02	(-0.07, −0.02)
Maximum shrub intercept length			
Intercept	163.21	14.85	(141.88, 184.54)
Ungulate	−0.66	0.19	(-0.94, −0.39)

[a] spatial autoregressive parameter.
[b] 5–15 cm depth.

individuals, whereas utilization distribution levels only reflect the collared individuals. Subsequently, because horses exhibited non-exclusive home ranges, utilization distribution levels of one band do not account for additional use of another. Without knowing the movements and group sizes for each band in the study area, we could not appropriately correct utilization distribution levels; thus, the number of fecal piles per sample location was a better metric of total horse use.

We did not find significant relationships between horse use and shrub cover, shrub fragmentation, shrub height, visual obstruction, and native perennial or cheatgrass cover. This does not definitively indicate that horse use does not affect these characteristics. We attempted to limit topographic variation in our sampling design, yet topographic characteristics were still informative predictors of some metrics, suggesting that more restrictive topographic variation in sampling was warranted. Perhaps more importantly, we did not sample sites without horse use. We know that the variables we evaluated often differ between grazed and un-grazed sites (e.g., Beever and Brussard, 2004; de Villalobos and Zalba, 2010), consequently reference sites without active grazing may be needed to detect differences in these metrics but such sites may also be inherently unpreferred for certain features, further confounding measurements. The lack of grazing exclosures may be a reason why we did not detect a correlation between grass cover and feral horse use. The digestive physiology of horses necessitates a high-intake strategy (Janis 1976), particularly of graminoids; thus, we would expect increased horse use in areas with higher grass cover. Therefore, our methods may not have been able to differentiate between sites with low grass cover due to herbivory and sites with inherently low grass cover due to abiotic factors.

5. Conclusion

Livestock management on private and public lands involves grazing systems that routinely incorporate recovery and/or rest periods for pastures and allotments (NRCS, 2016). This respite from grazing disturbance is fundamental to grazing management because it allows for plant recovery and long-term sustainability of rangeland health (Danvir, 2018; Jacobo et al., 2006). Our study indicates that decreased horse use may reduce the potential for soil erosion and positively influence cover for sage-grouse, but management of population size alone is likely ineffective for maintaining other aspects of habitat quality because repeated use of the same areas, regardless of population size, has negative implications on ecosystem services. The Federal Land Policy and Management Act of 1976, mandates federal agencies to manage public lands to support multiple uses, including feral horse, livestock, and wildlife habitat (Public Law 94–579, 1976). Manipulation of when and where horses graze, in addition to population management, is recommended to sustain wildlife habitat quality within herd management areas into the future.

CRediT authorship contribution statement

Jacob D. Hennig: Conceptualization, Methodology, Validation, Formal analysis, Data curation, Writing – original draft, Project administration, Visualization. **Jeffrey L. Beck:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Courtney J. Duchardt:**

Conceptualization, Investigation, Writing – review & editing. **J. Derek Scasta:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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