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Nonnative ungulate impacts on greater sage-grouse late brood-rearing habitat in the Great Basin, USA

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Abstract: Domestic livestock grazing is the dominant land use on much of the current range inhabited by greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) in the western United States. Nonnative feral horses (*Equus ferus caballus*) also inhabit important sage-grouse seasonal habitats. Overabundant feral horse populations and improper grazing by domestic cattle (*Bos taurus*) can impact the health of sagebrush (*Artemisia* spp.) and desert shrub rangeland communities and native wildlife. These impacts to sage-grouse can be exacerbated when they affect late brood-rearing habitat, which provide the forbs and arthropods required to fledge broods. Managers require better information regarding the extent of these impacts. In 2020, we assessed the potential impact of feral horses and domestic cattle on sage-grouse late brood-rearing habitats in western Utah and eastern Nevada, USA. We acquired late brood-rearing location data from sage-grouse marked with global positioning system and very-high frequency radio-transmitters from 2016 to 2020 for North Utah data, 2017 to 2018 for South Utah data, and 1961 to 2017 for both east and west Nevada data to delineate late brood-rearing habitats. Using these location data, we compared 8 sites (4 pairs) within horse and non-horse use areas to assess sage-grouse habitat quality characteristics between areas that have been predominantly horse and cattle grazed versus sites that have been predominantly cattle grazed. For each pairing, 1 site was located within and the other outside of a Bureau of Land Management herd management area boundary, and both sites shared similar habitat characteristics (i.e., topography, dominant vegetation, soils, and climate) and selection probability for broods. We collected vegetation and dung count data at each site to assess characteristics related to habitat quality for sage-grouse brood-rearing, based on ungulate presence. We used a mixed model analysis of variance to detect differences between each paired site comparison ($\alpha < 0.01$). Horses or evidence of horse presence (i.e., dung) were not detected at our non-horse sites allowing for an unbiased comparison between paired sites. Cattle presence was noted at all our paired sites. Average annual grass frequency was 0.74 in horse and 0.17 in non-horse use areas ($P = 0.20$), and average annual grass cover was 4.0% compared to 0.2% in horse use areas ($P = 0.32$). Average annual grass biomass was 0.45 kg/ha in horse and 0.04% in non-horse use areas ($P = 0.34$). Vegetation height was 44.2 cm in non-horse compared to 34.5 cm in horse use areas ($P = 0.23$). These results suggest that increased ungulate grazing and year-long use of late brood-rearing habitat by feral horses coupled with livestock grazing may impair habitat suitability, particularly considering ecological impacts from invasive plant species. Our results suggest that managing late brood-rearing habitats to reduce the frequency and intensity of year-long grazing by feral horses can be best accomplished by reducing horse numbers and the seasonal distribution of grazing by domestic livestock.

Key words: *Artemisia* spp., *Bos taurus,* brood-rearing, cattle, *Centrocercus urophasianus*, *Equus ferus caballus*, feral horses, Great Basin, greater sage-grouse, sagebrush

Feral and domestic animals can pose threats to native biodiversity and conservation efforts throughout the world (Beever et al. 2019). Grazing by domestic livestock is the predominant anthropogenic land use internationally, affecting 10–60% of differing rangeland types worldwide (Alkemade et al. 2012), and can influence rangeland ecosystem services and the quantity and quality of wildlife habitat (Dettenmaier 2018). In addition, the environmental impacts of feral horses (*Equus ferus caballus*; horses) are increasingly becoming an international conservation concern (Schoenecker et al. 2021).

In the United States, horses are considered by biologists to be an invasive species (The Wildlife Society 2020). Overabundant feral horses can impact rangeland health and ecological resilience within arid and semi-arid areas in North America (Davies and Boyd 2019, Eldridge et al. 2020, Hennig et al. 2021). In contrast, the greater sage-grouse (*Centrocercus urophasianus;* hereafter sage-grouse) is a native North American wildlife species that relies on sagebrush (*Artemisia* spp.) habitats (Knick and Connelly 2011). Populations of sage-grouse have been in decline for more than the past 6 decades, primarily in response to lost and fragmented habitat attributed to resource exploitation, development, over-utilization of rangelands, invasive species, predation, and altered fire regimes (Connelly et al. 2000, 2004; Crawford et al. 2004; Aldridge et al. 2008; Kaczor et al. 2011; Miller et al. 2011; Conover and Roberts 2016). The most dominant land use of the current range inhabited by sage-grouse in the western United States is domestic livestock grazing (Knick et al. 2003). Direct competition for forage plants and indirect competition through habitat disturbance associated with nonnative ungulate grazing and trampling may impact the fitness of sage-grouse through altered habitat as horses and sage-grouse typically inhabit similar areas (Beever and Aldridge 2011, Davies and Boyd 2019, Hennig et al. 2021).

Following their extirpation and extinction in North America at the end of the Pleistocene Epoch, horses were transported by European explorers in the early 1500s to the Americas and other locations (Olsen 2016). In the areas where they were introduced, horse densities have increased as a result of high reproductive success, limited predation, and inadvertent or purposeful releases (Young and Sparks 2002, National Research Council 2013). Populations of horses have experienced continued steady growth since the passage of the Wild Free-Roaming Horses and Burros Act of 1971, further impacting limited resources in the arid western United States (National Research Council 2013, Scasta et al. 2018).

By March 2022, federally managed populations of feral equids on designated public lands in the western United States managed by the Bureau of Land Management (BLM) exceeded 64,600 horses (with 17,780 burros [*E. asinus*]) across 10 western states (BLM 2022). Schoenecker et al. (2021) estimated the national population in the United States to be almost 300,000 horses and burros across multiple land jurisdictions, with more feral horses found on sovereign tribal lands than on BLM or other public lands. Overabundant horse populations are often associated with degraded wildlife habitat, impaired ecosystem structure, and reduced rangeland health (Beever and Brussard 2000, Beever and Aldridge 2011, Davies et al. 2014, Hall et al. 2016, Davies and Boyd 2019, Eldridge et al. 2020, Hennig et al. 2021).

Horses differ from many of the domestic and wild ungulates found throughout western North America both in how their populations are managed and in their anatomy and physiology (Scasta et al. 2016). As a protected species, horses are not hunted (compared to most wild ungulates) and are not managed through seasonal grazing strategies (as domestic ungulates; Danvir 2018). As large hindgut fermenters, horses are potentially the least-selective ungulate herbivore as opposed to domestic cattle (*Bos taurus*) and their native ruminant counterparts bighorn sheep (*Ovis canadensis*), elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*; Beever 2003, Scasta et al. 2016). Less selective diets and more expansive home ranges compared to cattle may equate to reduced plant species diversity, impaired vegetation structure, and lower ecosystem resilience in horse-grazed areas compared to areas grazed by other ungulates (Beever 2003, Boyd et al. 2017). Additionally, a lower quality diet requires horses to consume 20–65% more forage than a ruminant of similar size (Menard et al. 2002). Subsequently, horses can alter sagebrush community structure, diminish vegetation composition, reduce soil stability, and displace native and sagebrush-obligate species (Ostermann-Kelm et al. 2009, Beever and Aldridge 2011, Hall et al. 2016, Gooch et al. 2017, Davies and Boyd 2019, Eldridge et al. 2020, Hennig et al. 2021).

Improper grazing by nonnative ungulates, including feral horses, has been implicated by the U.S. Fish and Wildlife Service (USFWS) as a conservation threat for some local sage-grouse populations (USFWS 2013). Although overgrazing by domestic cattle can produce environmental impacts similar to horses, the impacts are seasonal and the animals can be removed when adverse effects are observed (Danvir 2018). Ungulates degrade sage-grouse sagebrush habitats by reducing plant height and density and compacting soils that stem from excessive trampling and foraging (Beever and Aldridge 2011, Davies et al. 2014, Hall et al. 2016). Feral horses in particular have been shown to directly and indirectly impact sagebrush communities and impair local sage-grouse habitat quality and population densities (Coates et al. 2021, Muñoz et al. 2021), which can extend year-round and occur at broad landscape scales.

Sage-grouse females require specific habitats for brood-rearing to minimize risk and maximize nutrient requirements for their chicks (Dahlgren et al. 2015, 2016). Females with broods often select sites with increased vegetation cover and height (Hagen et al. 2007, Kaczor et al. 2011), particularly in areas where forbs, grasses, sagebrush, and insects are available (Casazza et al. 2011, Connelly et al. 2011). Improper nonnative ungulate grazing of these brood-rearing habitats is of significant concern to land managers responsible for maintaining and conserving sage-grouse populations. Late brood-rearing habitats are of particular concern because they sustain developing chicks by providing an abundance of succulent forbs and insects in the summer and fall as well as cover for avoiding predation (Crawford et al. 2004, Atamian et al. 2010, Kaczor et al. 2011, Dahlgren et al. 2019). These habitats are typically characterized by montane sagebrush, riparian shrubland, desert grassland, and big sagebrush where sage-grouse often select sites higher in elevation with more moisture and riparian shrubs or montane sagebrush (Braun et al. 1977, Kirol et al. 2012, Smith et al. 2018, Gelling et al. 2022). Although late brood rearing habitat has been found to be critical for sustaining sage-grouse populations, there is limited research that assesses the direct impacts of feral horses and domestic cattle on late brood-rearing habitat of sage-grouse (Street 2020).

The purpose of our study was to determine the effects of cattle and feral horse herbivory on big sagebrush (*A. tridentata*) and black sagebrush (*A. nova*) plant communities where sage-grouse brood-rearing was documented within the Great Basin region. Because horse and cattle herbivory effects on sagebrush ecosystems can be difficult to differentiate, we assessed changes in habitat structure in areas where horses and cattle co-mingled and compared these changes to areas only grazed by cattle. We hypothesized that combined horse/cattle utilization in these habitats would have a greater impact on vegetation structure and suitability of habitat for sage-grouse during late brood-rearing than cattle grazing alone. Specifically, we expected sites where horse and cattle co-mingled to have lower overall vegetation height, increased invasive species presence, and lower frequency and percent cover of grasses and forbs. Our goal in this study was to indirectly assess the structure of late brood-rearing habitat and its probable relationship to sage-grouse fitness and population patterns.

Study area

To conduct our study, we selected 8 study sites in 4 pairs (Benmore Pasture/Government Creek (north Utah pair), Butcher Troughs/Hamblin Wash (south Utah pair), High Schell/Spring Gulch (east Nevada pair), and Pony Express/Egan Canyon (west Nevada pair) located within Utah and Nevada, USA (Figure 1). Each study site was located in high elevation, cool desert ecosystems characterized by hot, dry summers and cold winters. Dominant shrubs typical for all study sites included: black sagebrush, broom snakeweed (*Gutierrezia sarothrae*), Wyoming big sagebrush (*A. t. wyomingensis*), and yellow rabbitbrush (*Chrysothamnus viscidiflorus*). Common grasses included: bottlebrush squirreltail (*Elymus elymoides*), cheatgrass (*Bromus tectorum*), crested wheatgrass (*Agropyron cristatum*), and Sandberg bluegrass (*Poa secunda*). Bur buttercup (*Ceratocephala testiculata*) was an annual forb common to all sites. Sites were located between approximately 1,676 and 2,014 m elevation, and paired distances ranged from 3–31 km from each other. Annual temperature and precipitation at these sites ranged between -10°C and 31°C and 0.76–3.30 cm, respectively

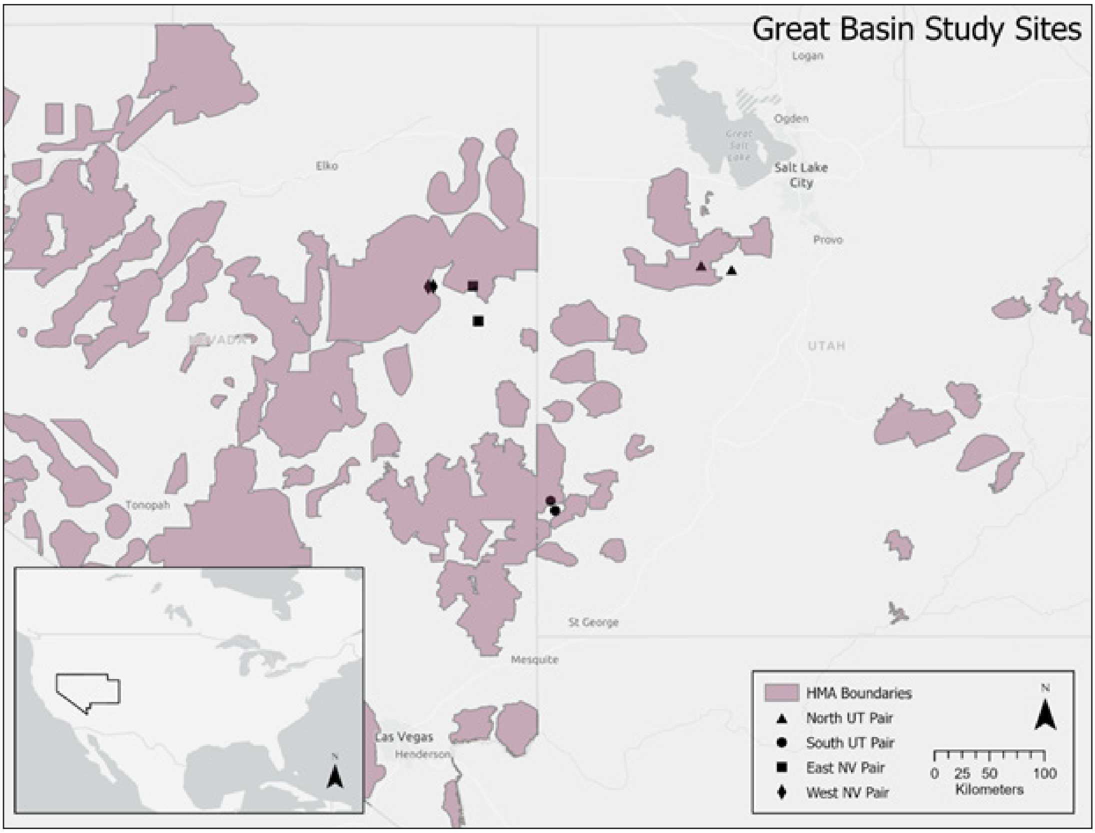

Figure 1. Eight study sites were compared in 2020 to determine differences in habitat characteristics. The sites included: north Utah (UT) pair (Benmore Pasture/Government Creek), south Utah pair (Butcher Troughs/Hamblin Wash), east Nevada (NV) pair (High Schell/Spring Gulch), and west Nevada pair (Pony Express/Egan Canyon).

(U.S. Climate Data 2020). These study sites were all located on public land where multiple-use activities occur.

The Nevada study sites were located within and near the Triple B and Antelope herd management areas (HMAs). The Triple B HMA was approximately 498,772 ha with an appropriate management level (AML) range of 250–518 horses. The west Nevada paired sites were located within and near the Triple B HMA with an estimated population of 1,030 horses, which was 199% above AML (BLM 2021). The Antelope HMA was approximately 161,777 ha with an AML range of 150–324 horses. The east Nevada paired sites were located within and around the Antelope HMA that had an estimated horse population of 2,100, 648% above AML (BLM 2021).

The Utah study sites were located within and near the Onaqui Mountain, Choke Cherry, and Sulphur HMAs. The Onaqui Mountain HMA is approximately 83,120 ha and had an AML range of 121–210 horses. The north Utah paired sites were situated within and around the Onaqui Mountain HMA, which was 226% above AML with an estimated horse population of 474. In southwestern Utah, Choke Cherry and Sulphur HMAs were located closest to the south Utah paired sites. The Choke Cherry HMA was approximately 19,481 ha with an AML range of 24–30 horses and an estimated population of 28 horses, which was within AML (BLM 2021). However, the Sulphur HMA was approximately 107,529 ha with an AML range of 165–250 and an estimated population of 414, which was 166% above AML (BLM 2021).

Methods

We selected 8 study sites to compare horse use with non-use areas by pairing late brood-rearing habitat within and outside of HMAs, respectively. Sites within HMAs exhibited

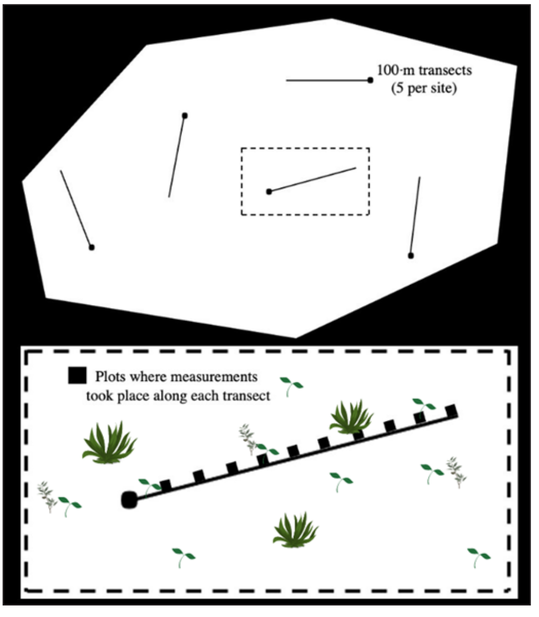

Figure 2. Within the delineated greater sage-grouse (*Centrocercus urophasianus*) late brood-rearing habitat areas at each of the 8 study sites, we established 5 randomly located plot center points. At each plot center, we extended a 100-m transect from which we systematically measured: (1) vegetation height (total height [including reproductive inflorescences] and vegetative height [overall plant height without reproductive material]), (2) vegetation biomass total and by species, (3) relative frequency of species and functional groups, (4) percent foliar cover of species and functional groups, (5) soil compaction, and (6) dung density (horse [*Equus ferus caballus*] and cattle [*Bos taurus*]). We measured all of the vegetation metrics in each plot along the left side of each transect to minimize plot disturbance (i.e., investigator trampling). Transect bearings were randomly oriented ranging in bearing between 0 and 359 degrees. In addition to the main transect at each random point, 2 more transects were extended from the random point to conduct dung pile and pellet group counts. All measurements at each site were taken between August 1, 2020 and October 2, 2020.

both horse and cattle grazing, while sites outside HMAs experienced only cattle grazing. To delineate late brood-rearing habitat ranges, we used coordinate locations obtained from radio-marked sage-grouse that were monitored yearlong within each area. We identified sage-grouse late-brood rearing areas in the north Utah portion of the study area using data collected from sage-grouse marked with a very-high frequency (VHF) and global positioning system (GPS) that were monitored between 2016 and 2020 by Utah State University (USU) researchers (IACUC #2560). All radio-marked individuals were monitored weekly from capture date to August and intermittently throughout the fall and winter.

Late brood-rearing locations were delineated as four weeks post-hatch to the designated 50-day brood age and ranged from June to July 2016 to 2020 (Thompson et al. 2006). Included in these north Utah data, where a translocation project was performed from 2016 to 2019, were 14 resident females' broods, 8 first-year translocated females' broods, and 14 second- and third-year post-translocation females' broods. Females in their second year post-release and greater typically exhibit habitat selection similar to residents, and brooding females within their first year post-release exhibited movements indicating residency behavior; thus, these data were deemed appropriate for use in the late brood-rearing sites for the north Utah data (Gruber-Hadden et al. 2016, Ebenhoch et al. 2019, Picardi et al. 2022, M. S. Chelak, unpublished data). The south Utah data were acquired from USU researchers with GPS-marked sage-grouse from June to August of 2017 to 2018 (IACUC #10175). Nevada late-brood rearing location data were obtained from the Nevada Department of Wildlife (NDOW) using a historic sage-grouse brood survey database, and we used late brood-rearing data from June to August of 1961 to 2017 with consistent monitoring data between 2013 and 2017.

Once late brood-rearing sites were identified, we created a minimum convex polygon to identify study area boundaries using ArcGIS Pro (Environmental Systems Research Institute, Inc. [ESRI], Redlands, California, USA). We then paired 4 selected late brood-rearing sites within HMAs to the nearest points outside of HMA boundaries with similar habitat characteristics. Sites were determined by assessing differential sage-grouse summer habitat selection through habitat selection analyses provided by researchers at USU for the Utah paired sites (USU, unpublished data) and at the U.S. Geological Survey Western Ecological Research Center for the Nevada paired sites (Coates et al. 2016, 2020; Brussee et al. 2022).

Sampling

Within the delineated late brood-rearing habitat area, we established 5 randomly located plot center points using ArcGIS Pro (ESRI; Figure 2). At each plot center, we extended a 100-

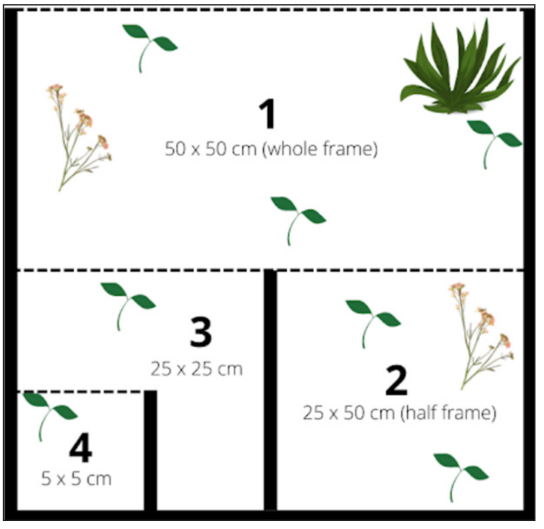

Figure 3. The nested frequency quadrat frame (0.25 m^2) we used at our 8 study sites in Utah and Nevada, USA, in 2020. When recording data for a nested frequency quadrat, the smallest quadrat in which the plant occurs is what is recorded. The smallest quadrat (4) on a nested frequency frame is 5x5 cm, and any plants located within this quadrat would by default occur in all the other quadrats. If a species fell within the smallest quadrat, it would be given a value of 4 as it is located within all 4 nested quadrats and is assumed to be more common on the landscape. If a species was only identified within the largest portion of the quadrat (1 [whole frame]), it would be given a value of 1 and assumed to be less common on the landscape.

m transect from which variables representing ecological structure important for sage-grouse late brood-rearing were sampled (Dahlgren et al. 2019). These metrics included: (1) vegetation height (total height [including reproductive inflorescences] and vegetative height [overall plant height without reproductive material]), (2) vegetation biomass (total weight by species), (3) species frequency, (4) percent foliar cover (nested frequency quadrat and line intercept methods), (5) soil compaction, and (6) dung density (horse and cattle). All metrics were measured in each plot along the left side of each transect to minimize plot disturbance (i.e., investigator trampling; Table 1). Transect bearings were randomly oriented, ranging in bearing between 0 and 359 degrees.

We recorded nested frequency of herbaceous vegetation (i.e., perennial/annual grasses, perennial/annual forbs) and soil surface properties (i.e., bare-ground, rock, litter) using a 0.25-m^2 nested frequency quadrat (Greig-Smith 1983; Figure 3). We placed a nested frequency quadrat along the transect at 10-m intervals for a total of 10 quadrats per transect. When recording data for a nested frequency quadrat, the smallest quadrat in which the plant occurs is what is recorded. The smallest quadrat (4) on a nested frequency frame is 5x5 cm, and any plants located within this quadrat would by default occur in all the other quadrats. If a species fell within the smallest quadrat, it would be given a value of 4 as it is located within all 4 nested quadrats and is assumed to be more common on the landscape. If a species was only identified within the largest portion of the quadrat (1), it would be given a value of 1 and assumed to be less common on the landscape (Figure 3). This method does not explicitly measure frequency as a percentage. Instead, frequency was expressed using a mean value ranging between 0 and 4, with lower values (closer to 1) suggesting lower frequency and higher values (closer to 4) suggesting higher frequency.

Using the nested frequency quadrat, we estimated percent cover of all the functional groups using predetermined points (pins) associated with the quadrat (Table 2). A nested frequency quadrat has 8 pins that point to specific areas within the quadrat. Each time the quadrat was set down, "hits" were recorded based on the functional group each pin was pointed at.

Shrubs and overall sagebrush cover were both measured simultaneously along the transect using the line intercept method. This gave us 2 measures of shrub cover for each site. We estimated maximum plant height by averaging the highest plant growth (including inflorescence) from all sampled plants per plot per transect. Similarly, we assessed maximum vegetative height based on non-reproductive (vegetative) material. We used a meter stick to measure height and averaged all respective heights along each transect. We measured relative soil compaction using a simple metal rod soil penetrometer (0.5-cm diameter) at 10-m intervals for a total of 10 times per transect. The same person measured depth penetration to provide consistency between measurements taken at different sites and plots.

We sampled plant biomass by clipping all above-ground plant tissue by species within quadrats equal in size to the nested frequency quadrat (0.25 m^2). We grouped species into

Table 1. Metrics used to assess habitat quality characteristics of greater sage-grouse (*Centrocercus urophasianus*) between sites that have been predominantly horse (*Equus ferus caballus*) grazed versus sites that have been predominantly cattle (*Bos taurus*) grazed, at 8 study sites in Utah and Nevada, USA, 2020. The importance of each metric is listed along with the predicted response as it relates to increased horse use. Adapted from Hennig et al. (2021).

Habitat quality metric	Importance to sage-grouse late brood-rearing	Predicted response	Justification citation
Annual grass[a, b]	Escape cover, nest concealment, indirect effects on habitat quality	Increase	Connelly et al. (2004)
Forbs[a]	Food resource	Decrease	Dahlgren et al. (2019)
Perennial grass[a]	Escape cover, nest concealment	Decrease	Aldridge and Boyce (2007)
Shrubs[a, c]	Escape cover, nest concealment, food resource	Decrease	Connelly et al. (2000), Crawford et al. (2004)
Litter[d]	Indirect effects on vegetation structure and habitat quality	Increase	Indirect effect
Non-living[d]	Indirect effects on habitat quality	Increase	Indirect effect
Soil compaction[e]	Indirect effects on habitat quality	Increase	Beever and Herrick (2006)
Plant height[f]	Nest and brood concealment, escape cover	Decrease	Connelly et al. (2000), Doherty et al. (2014)
Nonnative ungulate dung frequency[g]	Indirect effects on habitat quality	Increase	Beever and Aldridge (2011)

[a]Measured mean relative frequency, percent cover, and biomass of all functional groups found within nested frequency plots
[b]Cheatgrass (*Bromus tectorum*) was the only annual grass found along our transects.
[c]Measured using line intercept and nested frequency methods
[d]Relative percent cover
[e]Relative soil compaction
[f]Mean plant height (total and vegetative)
[g]Nonnative ungulates include horse and cattle, although we also recorded native ungulate and sage-grouse fecal material when found.

functional groups: shrubs, perennial grasses, annual grasses, and perennial and annual forbs combined. We clipped all above-ground living leaf tissue from plots at 2 locations along each transect (25 and 75 m) and placed the material into labeled paper bags. In the lab, we dried the material in a drying oven at approximately 21°C for 48 hours and then immediately weighed each dried sample (bag) to determine total dry weight plant biomass. We determined dry weight plant biomass to the species level for all plant groups. We recorded all measurements at each site between August 1, 2020 and October 2, 2020.

Ungulate presence

We counted dung from large ungulates at each site to develop an index for quantifying ungulate use at each location. At each random point, we implemented a wagon-wheel sampling design (3 100-m transects extending out from the predetermined given point 120° from each other) to count total dung by ungulate species. A predetermined bearing gave us 1 of 3 directions for the first transect (the other 2 transects were based on the first transect +/- 120°). Observers walked along the transect and stopped every 10 m along the 100-m transect to count all ungulate and sage-grouse dung piles within a 5-m radius (approximately 80 m^2) circular plot from the center point (10 per transect / 30 per point). Due to the irregular amount of fecal matter in defecations, concentrations of fecal matter were determined to be dung piles after inspecting relative numbers, location, direction, and distance to other dung piles. Adult male horses defecate in latrines (i.e., "stud piles"). We counted these latrines as a single deposit due to the difficulty in parsing out individual fecal piles within a latrine.

Table 2. Habitat variables associated with greater sage-grouse (*Centrocercus urophasianus)* habitat comparing the treatment effect (horse [*Equus ferus caballus*] use vs. non-use) at each paired site in Utah and Nevada, USA, in 2020. The difference estimate is the result from the means associated with horse use sites subtracted by non-use sites. Standard error estimates are associated with the mean differences. Positive estimates indicate higher values at the horse sites while negative estimates indicate higher values at the non-horse sites.

Variable	Non-horse $\bar{x}$	Horse $\bar{x}$	$\bar{x}$ Difference	SE	df	*t*	*P*
Nested frequency							
Annual grass	0.17	0.74	-0.56	0.34	3	-1.62	0.20
Dung	0.040	0.21	-0.17	0.07	3	-2.47	0.09
Forbs	1.37	1.45	-0.083	0.488	3	-0.17	0.87
Perennial grass	2.25	2.19	0.058	0.52	3	0.11	0.92
Shrubs	1.40	1.53	-0.136	0.12	3	-1.10	0.35
Cover (%)							
Annual grass	0.20	3.95	-3.75	3.18	3	-1.18	0.32
Forbs	1.85	2.00	-0.15	1.17	3	-0.13	0.91
Litter	23.20	20.60	2.60	4.01	3	0.65	0.56
Non-living	47.80	51.75	-3.95	6.41	3	-0.62	0.58
Perennial grass	13.35	8.45	4.90	5.75	3	0.85	0.46
Shrubs	13.75	13.25	0.50	2.00	3	0.25	0.82
Line intercept (cover)							
All shrubs	19.55	18.54	1.013	3.29	3	0.31	0.78
Sagebrush	18.36	15.75	2.61	3.45	3	0.76	0.50
Biomass (kg/ha)							
Annual grass	0.043	0.45	-0.41	0.37	3	-1.10	0.34
Forbs	2.41	4.91	-2.51	1.87	3	-1.34	0.27
Perennial grass	17.12	15.25	1.87	9.45	3	0.20	0.86
Shrubs	7.74	7.12	0.62	2.27	3	0.27	0.80
Soil compaction (cm)	6.53	6.74	-0.21	0.91	3	-0.23	0.83
Height (cm)							
Total	44.19	34.49	9.70	6.40	3	1.52	0.23
Vegetation	32.18	27.08	5.10	3.90	3	1.31	0.28
Dung (per 0.25 m^2 plot)							
Cattle	24.70	4.73	19.97	7.41	3	2.70	0.07
Horse	0.00	23.45	-23.45	7.10	3	-3.30	0.046
Other ungulate	0.33	0.55	-0.22	0.22	3	-0.96	0.41
Sage-grouse	0.42	1.00	-0.58	0.62	3	-0.95	0.41
Total ungulate	25.03	28.73	-3.70	3.18	3	-1.16	0.33

Use by horses and cattle was similar among paired sites, but sites within the HMAs were predominately used by horses while the other sites only exhibited cattle use. This allowed for a clear separation between horse use in a study site compared to the control (non-horse) while maintaining similar plant composition and proximity. This pairing approach reduced potential confounding factors resulting from ecological differences. If a pair was selected that did not have the same dominant plant species or environmental conditions as the other pair or pairs, it was removed from the analysis, and a new pair was selected.

Statistical analysis

We used a mixed model analysis of variance blocking on pairs with horse use versus non-use as the independent variable to detect differences between the comparison of plant functional groups and dung variables. We conducted data analysis using SAS v.9.4 software (SAS Institute Inc., Cary, North Carolina, USA).

Results

There were no differences in sagebrush cover comparing horse and non-horse use areas (difference of 2.61%, t-stats = 3.45, df = 3, P = 0.50). The relative nested frequency of annual grass in horse sites was 0.74 in horse compared to 0.17 in non-horse use areas (difference of 0.56±0.34, t-stats = -1.6, df = 3, P = 0.20), and the percent cover of annual grass in horse use areas was 4.0 compared to 0.2 in non-horse use areas (difference of 3.8±3.2, t-stats = -1.18, df = 3, P = 0.32). A similar difference was observed in annual grass biomass, which was 0.45 kg/ha in horse and 0.04 kg/ha in non-horse use areas (difference of 0.41±0.37 kg/ha, t-stats = -1.10, df = 3, P = 0.34). Total plant height was 44.2 cm high in non-horse areas compared to 34.5 cm in horse use areas, a difference of 9.7±6.4 cm (t-stats = -1.52, df = 3, P = 0.23). Height of just the vegetative growth was 32.2 cm in non-horse and 27.1 cm in horse use areas, a difference of 5.1 cm (t-stats = 1.31, df = 3, P = 0.28; Table 2).

As expected, overall dung frequency was higher in horse than non-horse use areas (P < 0.01). Horse dung frequency was 23.4 in horse use and 0 in non-horse use areas. In contrast, cattle dung frequency was 24.7 in non-horse compared to 4.7 in horse-use areas, a difference of 19.9±7.4 (t-stats = 2.70, df = 3, P = 0.07; Table 2). A summary of the mean comparisons between each paired site for all variables tested is provided side-by-side (Table 3; Figure 4).

Discussion

Our study sought to determine the potential influence of herbivory by nonnative ungulates (horses and cattle) on late brood-rearing habitat for sage-grouse. We hypothesized that feral horse utilization in conjunction with cattle grazing in these habitats would decrease the structure and suitability of habitat for sage-grouse during late brood-rearing, potentially impacting local population stability.

We predicted areas with heavier grazing and trampling to have less suitable habitat conditions that could potentially lead to lower sage-grouse densities, likely due to lower chick survival and recruitment rates. We determined that annual grass frequency, percent annual grass cover, total and vegetation plant height, and dung frequency and density were all meaningful comparisons. We did not detect a meaningful or significant difference in soil compaction or shrub cover. The lack of difference in some comparisons was likely attributable to low sample size. However, these differences were practically important and biologically meaningful as they demonstrate substantially higher annual plant frequency and cover values in horse and cattle presence sites compared to just cattle presence sites alone. Based on our results, we postulate that intense ungulate grazing and the combined utilization of late brood-rearing habitat by feral horses and livestock may decrease sage-grouse brood-rearing habitat suitability. These results corroborate research on feral horses' effects on sage-grouse habitat (Davies and Boyd 2019, Hennig et al. 2021).

Average annual grass cover and frequencies, dominated by cheatgrass, were greater in horse use versus horse non-use areas. These results are consistent with previous studies that reported similar changes in vegetation community structure in areas that exhibited overabundant horse populations (Beever and Aldridge 2011, Boyd et al. 2017). The establishment and dominance of cheatgrass may indicate an ecological disturbance and lower habitat quality (King et al. 2019, de Villalobos and Zalba 2010). Cheatgrass invasion is considered a significant ecological issue throughout the Great Basin (Mack 1981, Knapp 1996, Smith et al. 2022). Cheatgrass has invaded and established monoculture plant communities in many areas, often leading to reduced perennial plant diversity, disrupted vertebrate and invertebrate communities, and exacerbated fire regimes in the Great Basin (Knapp 1996, Balch et al. 2013, Chambers et al. 2014, Freeman et al. 2014, Holbrook et al. 2016, Cumberland et al. 2017, Bradley et al. 2018, Williamson et al. 2020). Increased fire and decreased biodiversity associated with increased cheatgrass presence may negatively impact sage-grouse habitat and recruitment (Connelly et al. 2011, Miller et al. 2011, Chambers et al. 2014).

Table 3. Means and standard errors of overall data collected at 8 Utah and Nevada, USA, study sites, 2020. Sites are paired up by horse (*Equus ferus caballus*; $n = 4$) and non-horse ($n = 4$) use sites (i.e., Benmore Pasture/Government Creek). Horse sites are designated with an asterisk (*).

Variable	Benmore Pasture	Government Creek*	Butcher Troughs	Hamblin Wash*	High Schell	Spring Gulch*	Pony Express	Egan Canyon*
Nested frequency								
Annual grass	0.12±0.03	1.66±0.23	0.00±0.00	0.45±0.30	0.12±0.05	0.05±0.05	0.46±0.23	0.78±0.21
Dung	0.00±0.00	0.38±0.11	0.12±0.06	0.24±0.10	0.00±0.00	0.14±0.07	0.04±0.03	0.09±0.04
Forbs	0.86±0.22	0.78±0.21	1.77±0.24	2.69±0.19	0.51±0.15	1.20±0.31	2.34±0.08	1.14±0.19
Perennial grass	3.51±0.05	2.40±0.19	2.96±0.07	2.48±0.19	1.16±0.11	1.16±0.12	1.36±0.25	2.72±0.08
Shrubs	0.25±0.11	0.64±0.17	1.90±0.23	1.88±0.23	1.63±0.08	1.87±0.14	1.81±0.19	1.74±0.20
Cover (%)								
Annual grass	0.00±0.00	13.40±3.87	0.00±0.00	0.60±0.60	0.00±0.00	0.00±0.00	0.80±0.37	1.80±0.73
Forbs	3.20±1.11	0.00±0.00	3.60±1.44	5.80±0.92	0.00±0.00	0.60±0.40	0.60±0.24	1.60±0.40
Litter	33.20±3.01	28.20±1.91	23.80±2.06	13.80±2.33	11.60±2.16	20.40±1.89	24.20±2.54	20.00±3.29
Non-living	25.80±3.50	35.80±6.00	44.80±4.37	62.60±2.50	70.40±2.01	58.60±2.91	50.20±4.21	50.00±2.51
Perennial grass	37.20±1.59	18.20±1.80	13.40±4.48	5.00±0.71	1.40±0.24	1.40±0.75	1.40±0.68	9.20±1.32
Shrubs	1.40±0.51	4.80±0.58	14.20±2.69	11.80±1.71	16.60±0.81	18.80±1.56	22.80±3.26	17.60±2.11
Line intercept								
All shrubs	3.19±1.39	9.33±3.98	16.50±2.03	13.27±0.99	24.83±3.62	26.91±1.81	33.69±1.56	24.65±2.47
Sagebrush	1.15±0.61	7.78±3.81	14.65±2.02	11.38±0.90	24.66±3.69	20.96±3.15	32.99±1.57	22.88±3.11
Biomass (kg/ha)								
Annual grass	0.02±0.02	1.57±1.43	0.00±0.00	0.05±0.03	0.02±0.02	0.05±0.05	0.13±0.13	0.15±0.10
Forbs	0.91±0.38	0.88±0.53	7.93±3.05	6.64±2.90	0.00±0.00	6.41±2.23	0.78±0.18	5.72±1.77
Perennial grass	42.06±6.15	50.22±37.71	21.67±7.59	7.85±3.19	4.40±1.72	1.04±0.71	0.32±0.17	1.88±0.47
Shrubs	4.81±2.95	9.35±5.64	8.62±2.85	10.23±4.61	7.49±2.09	2.76±0.76	10.06±0.32	6.16±1.67
Soil compaction (cm)	6.80±0.43	5.71±0.32	5.28±0.26	6.36±0.27	6.40±0.13	9.02±0.61	7.62±0.14	5.85±0.36
Height (cm)								
Total	49.61±2.29	45.21±7.39	52.73±2.57	24.18±1.41	31.38±1.39	31.32±1.10	43.02±3.20	37.23±1.02
Vegetative	33.73±1.70	32.70±4.70	33.31±2.72	17.51±1.05	24.95±1.56	26.94±1.15	36.74±2.77	31.18±1.10
Dung (per 0.25-m^2 plot)								
Cattle (*Bos taurus*)	44.67±8.97	5.07±0.81	32.07±5.95	9.20±0.87	13.07±3.48	2.07±0.92	9.00±1.09	2.60±0.64
Horse	0.00±0.00	41.67±3.73	0.00±0.00	27.73±1.89	0.00±0.00	12.93±3.28	0.00±0.00	11.47±2.72
Other ungulate	0.20±0.13	0.27±0.16	0.07±0.07	0.53±0.17	1.07±0.78	0.80±0.25	0.00±0.00	0.60±0.29
Sage-grouse (*Centrocercus urophasianus*)	0.67±0.30	2.73±0.66	0.80±0.58	0.00±0.00	0.20±0.20	1.20±0.53	0.00±0.00	0.07±0.07
Total ungulate	44.87±8.95	47.00±4.35	32.13±5.93	37.47±2.28	14.13±3.58	15.80±4.14	9.00±1.09	14.67±2.19

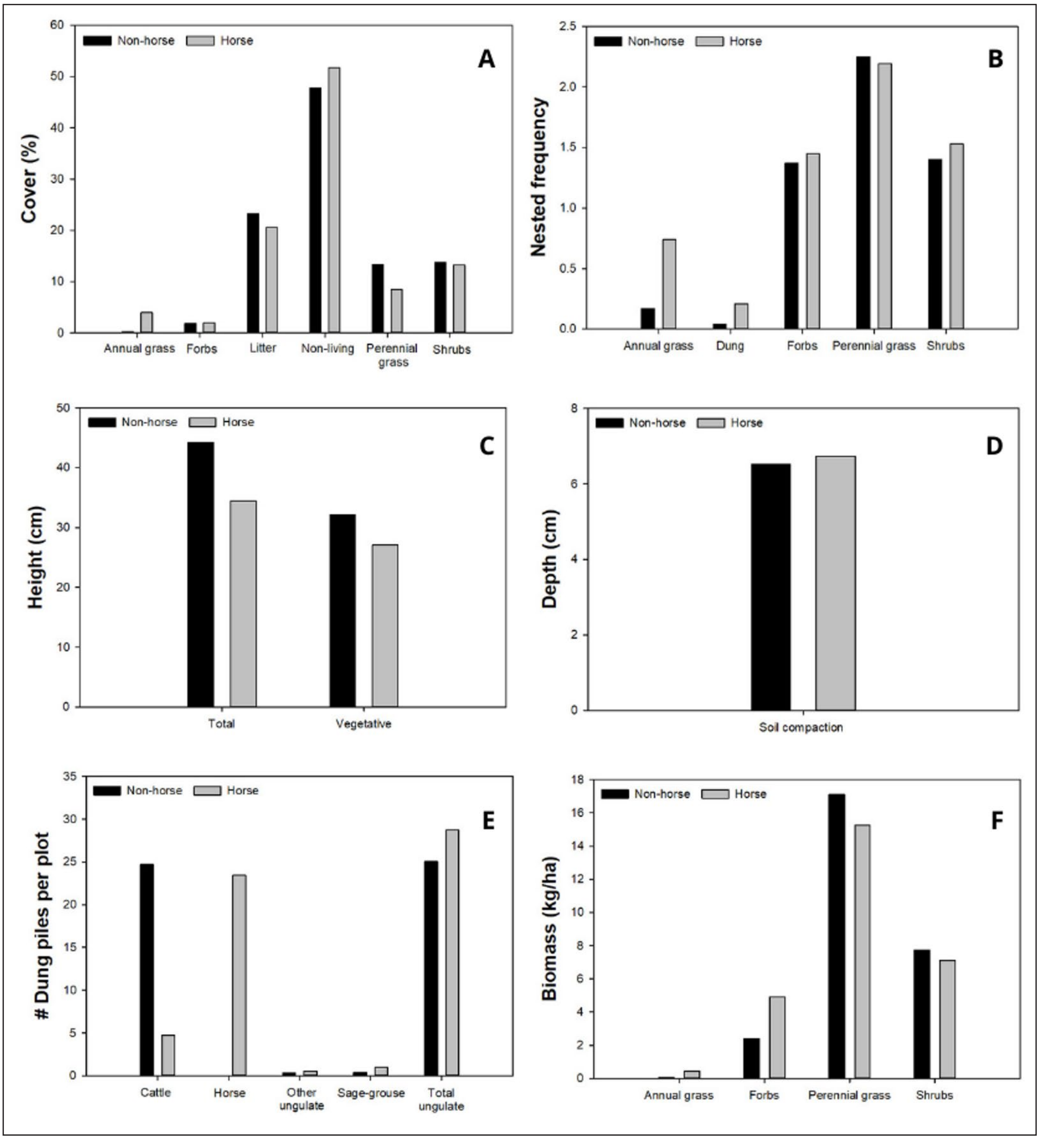

Figure 4. Comparison of all measurements between horse (*Equus ferus caballus*) and non-horse use sites throughout Utah and Nevada, USA, in 2020. (A) Percent foliar cover by functional groups. (B) Relative nested frequency values (the higher the value, the higher the relative frequency; the lower the value, the lower the relative frequency). (C) Plant height (total height is the overall height that includes reproductive inflorescences, vegetative height includes overall plant height without reproductive material). (D) Soil compaction depth measured in centimeters using a soil penetrometer. (E) Number of dung piles per 5-m plot. (F) Biomass.

Total plant and vegetation plant height were higher in non-horse use areas. This could suggest that combined horse and cattle grazing could impact the fitness of sage-grouse chicks through reduced plant height and increased cheatgrass abundance. Kaczor et al. (2011) determined that their most competitive resource selection model for broods in the Great Basin included maximum grass height, total herbaceous cover, and sagebrush height, where grass height and total herbaceous cover were positively associated with brood-rearing site selection. Other studies have also reported that vertical vegetation structure was negatively influenced by horse presence (Beever and Brussard 2000, Boyd et al. 2017, Hennig et al. 2021).

Reduced vegetation plant height and cover were found to reduce sage-grouse nesting and brood-rearing success (Hagen et al. 2007, Holloran et al. 2010).

Perennial grasses and forbs are important for cover and food sources for sage-grouse chicks through their associated insect abundance (Atamian et al. 2010, Dahlgren et al. 2015). In our study, perennial grass cover, frequency, and biomass as well as shrub biomass were lower at horse/cattle presence sites than at cattle presence sites alone. Although differences between sites were not statistically significant, it may suggest that the combined effect of horses and cattle in horse use sites degrades late brood-rearing habitat more than cattle alone. Davies et al. (2014) noted reduced perennial grass cover in heavily grazed sites, and Boyd et al. (2017) suggested a negative correlation between plant biomass and horse presence. Similarly, Street (2020) reported that increases in horse and cattle grazing resulted in decreased herbaceous understory, higher percent bare ground, and increased cheatgrass abundance, all resulting in suboptimal conditions for raising chicks. Street (2020) concluded that sage-grouse and their chicks will not or cannot avoid these areas, leaving chicks within degraded habitat vulnerable during this critical age-class. Atamian et al. (2010) reported that sage-grouse late brood-rearing areas are commonly dominated by montane sagebrush, riparian shrubland, desert grassland, and big sagebrush. These were common characteristics of the study sites we included in this study (Gillette et al. 2013, Robinson and Messmer 2013, Picardi et al. 2020).

Ostermann-Kelm et al. (2009) suggested that reduced vegetation cover and compacted soils were often associated with horse trailing. Furthermore, Davies et al. (2014) and Beever and Aldridge (2011) noted greater soil compaction and lower shrub density in areas with horses. We did not notice significant soil compaction or shrub cover differences between sites. However, soil was slightly more compacted at the non-horse sites than at the horse sites. These differences may be due partly to cattle presence in our non-horse sites and differences in research questions and methodologies. High sand content in the soil may also contribute to reduced compaction or minor differences in compaction at both sites.

Horse use sites that exhibit higher annual grass frequency and cover, lower plant height, lower vegetation height, and lower perennial grasses within these sage-grouse late brood-rearing areas could affect late-season brood survival, subsequent recruitment and, therefore, population trends (Casazza et al. 2011, Street 2020). Coates et al. (2021) found that increased horse abundance negatively impacted sage-grouse populations across the state of Nevada, and this research contributes to increasing understanding underlying some of the mechanisms behind the degradation of sage-grouse habitat and accompanying declines in sage-grouse abundance with associated horse presence (Street 2020, Hennig et al. 2021). Evaluating these mechanisms of feral horse effects on species of concern will be integral as climate change alters the systems in which they reside, especially within the Great Basin, where the interaction of invasive annual grasses, fire, and moisture availability is compounded (Chambers and Wisdom 2009, Boyte et al. 2016, Snyder et al. 2019).

While this study provides insight into the impacts of nonnative ungulates on brood-rearing habitat for sage-grouse, some limitations can be addressed in future research. In our study, no ungulates and not all sage-grouse broods were individually tracked (i.e., VHF or GPS transmitters); therefore, we could not determine the precise timing and movement patterns of ungulates and broods throughout the brood-rearing period. This lack of coordinate location data for ungulates made it difficult to parse the differences between horse and livestock use. Additionally, our study was limited to western Utah and eastern Nevada with limited replication. Optimally, this study could be expanded to a broader spatiotemporal scale to more precisely assess ungulate impacts that directly influence habitat where sage-grouse and horses overlap.

We also recognize that differences in annual grass cover were driven primarily by our data collected at the Benmore/Government sites, plant height was driven by data from Butcher/Hamblin sites, and that sample sizes were relatively small. In addition, there were significant temporal discrepancies between the brood location data in the Nevada and south Utah study sites and vegetation sampling, and we sampled brooding areas in the Utah study sites a few months later than brood location data. Logistics prevented us from vegetation sampling concomitantly with late brood-rearing locations; however, we still feel this study can provide some insight and noteworthy results, especially the marginally higher annual grass cover and lower sagebrush cover in all but 1 of the horse-occupied sites. Finally, reporting data from a long-term study could improve our interpretation of habitat impacts that vary from annual climate variability.

Management implications

Unmanaged and overabundant ungulate grazing in arid and semi-arid habitats can disrupt habitat conditions and suitability for sagebrush-obligate species. In our study, horse and non-horse use sites differed relative to annual grass frequency and cover, plant height, and horse and cattle dung frequency. Understanding this relationship can aid rangeland managers in identifying notable habitat differences in areas grazed by horses and cattle as compared to those with cattle-only grazing pressure. With this information, managers can understand how to manage ungulate densities to reduce impacts more effectively and promote better rangeland habitat for native species of concern.

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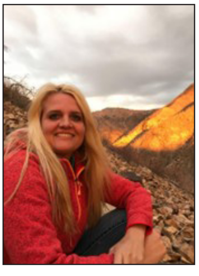

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