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Habitat selection and space use overlap between feral horses, pronghorn, and greater sage-grouse in cold arid steppe

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Abstract

Populations of feral horses (*Equus ferus caballus*) in the western
United States have increased during the past decade,
consequently affecting co-occurring wildlife habitat. Feral
horses may influence 2 native wildlife species, greater sage-
grouse (*Centrocercus urophasianus*; sage-grouse) and pronghorn
(*Antilocapra americana*) through mechanisms of habitat altera-
tion and competition. Wyoming, USA, contains the largest
populations of pronghorn and sage-grouse of any state and
also has the highest degree of range overlap between feral
horses and these species. Consequently, the effects that
horses may have on pronghorn and sage-grouse populations
in Wyoming have implications at local, state, and population-
wide levels. Managers need information concerning habitat
selection and space use overlap among these species to
develop appropriate management strategies; yet this informa-
tion is absent for most feral horse management areas. To
address this knowledge need, we attached global positioning
system (GPS) transmitters to horses, pronghorn, and sage-
grouse within the greater Bureau of Land Management–Adobe
Town Herd Management Area in southern Wyoming and
northern Colorado, USA, between 2017 and 2021 to evaluate
habitat selection and space use of all species during
3 biologically relevant seasons: spring (Apr–Jun; sage-grouse
breeding, nesting, and early-brood rearing; pronghorn late
gestation and early parturition), summer (Jul–Oct; sage-grouse
summer and late-brood rearing; pronghorn late parturition and

breeding), and winter (Nov–Mar; non-breeding season). Feral horses selected flatter slopes and shorter mean shrub height across all seasons and were closer to water in spring and summer. Pronghorn habitat selection was similar to horses, but they also avoided oil and gas well pads year-round. During spring, sage-grouse selected greater herbaceous cover, flatter slopes, and areas farther from well pads. In summer, sage-grouse selected greater mean shrub height, flatter slopes, and were closer to water. In winter, sage-grouse selected flatter slopes and areas with greater vegetation production during the preceding summer. Our results indicate strong year-round overlap in space use between horses and pronghorn, whereas overlap between horses and sage-grouse is greatest during the summer in this region. Consequently, managers should recognize the potential for horses to influence habitat quality of pronghorn and sage-grouse in the region.

Management of controversial feral animals is an increasingly common challenge in the Anthropocene (Boyce et al. 2021). In the western United States, feral horse (*Equus ferus caballus*) populations have increased within the past decade, threatening provision of ecosystem services (Scasta et al. 2018). Potential competition between cattle and feral horses has been a concern because of strong diet overlap and potential for horses to decrease rangeland quality (Beever et al. 2008, Scasta et al. 2016). Feral horse grazing can decrease vegetation biomass, increase soil compaction, increase proportion of bare ground, and facilitate the spread of invasive species (Beever et al. 2008, Davies et al. 2014, King et al. 2019, Hennig et al. 2021a). The direct and indirect effects that feral horses may have on native fauna is less understood. Habitat alteration and interference competition from feral horses can combine to potentially reduce habitat quality for co-occurring wildlife (Beever and Aldridge 2011, Gooch et al. 2017), but more critical investigations are imperative for management of co-occurring wildlife populations (Danvir 2018). The frequency and degree of horse-related effects are projected to increase because of increasing herd sizes (Davies and Boyd 2019); therefore, there is a pressing need to better understand area-specific potential for feral horses to affect wildlife species, especially species of concern.

Despite the potential negative effects of feral horses on rangelands, controlling population sizes or manipulating the distribution of feral horses to mitigate their detrimental effects is complicated because of their protected status under the Wild Free-roaming Horses and Burros Act of 1971 (Public Law 92-195 1971). This federal legislation designates horses and burros as natural components of western ecosystems because of their cultural significance to many United States citizens (Public Law 92-195 1971). The Act mandates the Bureau of Land Management (BLM) and the United States Forest Service (USFS) to balance feral equid populations with the ecological integrity of western rangelands, and the requirement to maintain the free-roaming status of feral equids limits management options (Public Law 92-195 1971). Further, limited budgets, lawsuits, declining adoption demand, and frequent vocal opposition to proposed management actions have combined to hinder the federal government's ability to control expanding feral equid populations.

Several feral horse Herd Management Areas (HMA) overlap with the distributional range of pronghorn (*Antilocapra americana*; Stoner et al. 2021), and greater sage-grouse (*Centrocercus urophasianus*; sage-grouse; Beever and Aldridge 2011), 2 wildlife species that have experienced range contraction, and in the case of sage-grouse, population decline (Yoakum and O'Gara 2000, Coates et al. 2021b). Wyoming, USA, contains >50% of the global pronghorn population and approximately 40% of the sage-grouse population (Yoakum and O'Gara 2000, Doherty et al. 2010), making management efforts for these species within Wyoming a major priority at local, state, and population-wide levels. Wyoming also contains the third highest abundance of feral horses, and of all the western states, the degree of range overlap between feral horses and pronghorn and sage-grouse is greatest within Wyoming (Beever and Aldridge 2011, BLM 2021, Stoner et al. 2021). Considering the high degree of range overlap, both species may be susceptible to habitat degradation, competition from horses, or both.

There is sparse but emergent information concerning the influence feral horses have on sage-grouse (Muñoz et al. 2021, Coates et al. 2021a, Hennig et al. 2021a), and multiple sources have listed horses as a potential threat to sage-grouse populations (Beever and Aldridge 2011, Southwest Wyoming Local Sage-grouse Working Group 2013, U.S. Fish and Wildlife Service 2013, South Central Sage-grouse Local Working Group 2014). Sage-grouse populations have declined in HMAs with feral horse abundances consistently above the legislatively imposed appropriate management level (AML; Coates et al. 2021a). Feral horses can directly affect sage-grouse by disturbing them during lekking (Muñoz et al. 2021) but are mainly thought to indirectly affect them through habitat alteration. Feral horses most likely affect pronghorn by competing with them for water or forage. In water-limited regions, the presence of feral horses can result in pronghorn being more vigilant at water (Gooch et al. 2017) or altering their use of water sources to decrease overlap with horses (Hall et al. 2018). Though the feeding and digestive strategies of horses (bulk-grazer and cecal digester; Janis 1976) and pronghorn (concentrate feeder and rumen digester; Van Soest 1994) differ, forage competition is a concern at sites with limited herbaceous production, especially during winter (Krysl et al. 1984, Stephenson et al. 1985, Scasta et al. 2016).

Though the ranges of feral horses, pronghorn, and sage-grouse overlap in Wyoming, an examination of habitat selection and space use overlap within HMAs is absent. Such information could identify seasonally important resources for each species and elucidate areas where potential habitat alteration and competition from horses may be greatest. To address this need, we studied habitat selection and space use of co-occurring feral horse, pronghorn, and sage-grouse populations within the greater Adobe Town HMA in southern Wyoming and northern Colorado, USA. Our objectives were to assess seasonal habitat selection for each species, create spatially explicit seasonal maps of predicted use per species, and estimate space use overlap between these species seasonally.

STUDY AREA

We conducted our study within the greater Adobe Town HMA in southern Wyoming and northern Colorado (2,210 km², 41°10′N, −108°14′W; Figure 1). Our study area included the HMA boundary and the BLM livestock grazing allotments outside of the HMA where we documented individuals of all species (Figure 1). The study area lies within the Red Desert which is classified as cold arid steppe (Kottek et al. 2006) and characterized by hot, dry summers (May–Sep) and cold, snowy winters (Nov–Mar). Elevation ranged from 1,883–2,506 m (U.S. Geological Survey [USGS] 2016) and annual 30-year normal mean precipitation and temperature were 27.7 cm and 6.0°C, respectively (PRISM Climate Group 2021). The area was a shrubland-dominated ecosystem with desert salt-scrub communities (Gardner's saltbush [*Atriplex gardneri*], shadscale [*A. confertifolia*], rubber rabbitbrush [*Ericameria nauseosa*], yellow rabbitbrush [*Chrysothamnus viscidiflorus*], spiny hopsage [*Grayia spinosa*]) in the interior of the HMA, Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) stands dominating the periphery of the HMA, and greasewood (*Sarcobatus vermiculatus*) flats intermixed throughout the study area. The study area contained limited herbaceous production, but common species included prairie Junegrass (*Koeleria macrantha*), bottlebrush squirreltail (*Elymus elymoides*), Sandberg bluegrass (*Poa secunda*), and sandhill muhly (*Muhlenbergia pungens*). The AML for the
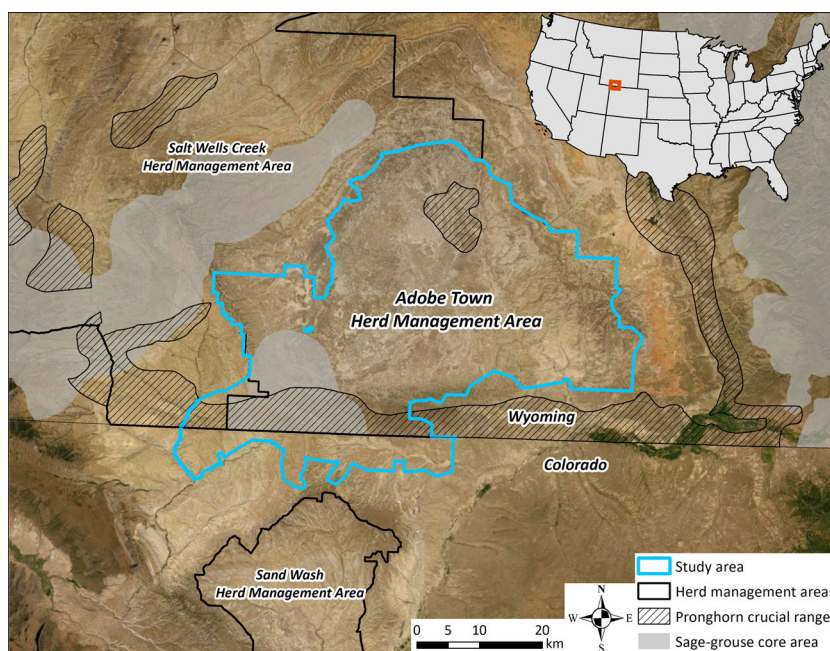
FIGURE 1 Location of the greater Adobe Town Herd Management Area, Wyoming and Colorado, USA. The area includes year-long and winter crucial ranges for pronghorn and core areas for greater sage-grouse (Wyoming Game and Fish Department), and is adjacent to the Salt Wells Creek Herd Management Area and close to the Sand Wash Herd Management Area. Background image source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

Adobe Town HMA is 610–800 horses, and the horse population was within AML in 2017–2018 but above AML from 2019–2021, the years of our study (BLM 2021). The region also contained core areas for greater sage-grouse (Doherty et al. 2011, State of Wyoming 2019) and areas classified by the Wyoming Game and Fish Department (WGFD) as crucial year-long ranges for pronghorn (WGFD 2021; Figure 1). There was a low amount of sage-grouse breeding habitat considered to be high-density (core area covered 11% of the study area), but there were portions of the study area that were included in adjacent sage-grouse core areas during the winter (Smith et al. 2014, 2019). The study area also provided habitat for elk (*Cervis canadensis*), mule deer (*Odocoileus hemionus*), white-tailed prairie dog (*Cynomys leucurus*), Brewer's sparrow (*Spizella breweri*), sagebrush sparrow (*Artemisiospiza nevadensis*), sage thrasher (*Oreoscoptes montanus*), loggerhead shrike (*Lanius ludovicianus*), and greater short-horned lizard (*Phrynosoma hernandesi*). Land uses included livestock ranching and fossil fuel exploration and extraction.

METHODS

Animal relocation data

We deployed oval-shaped iridium-based global positioning system (GPS) collars (Lotek Wireless IridiumTrackM 3D collars, Lotek Wireless, Newmarket, Ontario, Canada; and Vertex Lite GPS collars, Vectronic Aerospace GmbH, Berlin, Germany) on adult female horses residing in the Adobe Town HMA between February and October 2017, and round-shaped store-on-board GPS collars (model G2110D; Advanced Telemetry Systems, Isanti, MN, USA) on adult female pronghorn in November 2017. The collars used on horses and pronghorn weighed approximately

1,080 g and 410 g, respectively. We captured feral horses via bait-trapping and helicopter gathers and attached collars while animals were restrained in a hydraulic squeeze chute. We used helicopter net-gunning to capture adult female pronghorn (Native Range Capture Services, Ventura, CA, USA) and fit collars at the capture location. We programmed GPS transmitters to record locations every 2 hours (12 locations/day) for horses and every 4 hours (6 locations/day) for pronghorn and set all collars to remotely detach after 2 years. Beginning in March 2018, we deployed rump-mounted GPS transmitters (22-g GPS PTT, GeoTrack, King George, VA, USA; and 15-g Bird Solar, e-obs GmbH, Grunwald, Germany) on female sage-grouse captured within our study area through spot-lighting and hoop-netting (Smith et al. 2016). We continued to capture and attach transmitters to sage-grouse each December and April 2018–2020.

We rarefied locations to be consistent with transmitters that collected the fewest number of locations, which was 4–6 locations/day depending on time of year (Pratt et al. 2017). Prior to analyses, we subsampled our 2-hour fix rate of horses to a 4-hour fix rate to match the fix rate for GPS collars affixed to pronghorn. Because sage-grouse fixes were variable between transmitter types and seasons, we resampled sage-grouse locations to include 1 location at night (0000–0400 Mountain Standard Time [MST]) and 3–5 locations during the day (0700–1900 MST; ~ every 3 hours; Pratt et al. 2017), which matched the transmitters with the sparsest fix rate.

Season classification and spatial predictor variables

Sage-grouse habitat selection differs seasonally (Fedy et al. 2014), with distinct habitat preferences during the breeding, summer, and winter seasons (Connelly et al. 2011, Pratt et al. 2019). We followed methodology set forth by Pratt et al. (2017) to set date cutoffs for each season. This involved fitting double-logistic curves of net-squared displacement by date to identify migratory individuals (Bunnefeld et al. 2011, Singh et al. 2016). We used the mean leave and return dates from winter ranges for migratory individuals to delineate the winter season for the entire population. We performed these analyses using the nlme (Pinheiro et al. 2021) and adehabitatLT packages (Calenge 2006) in R version 4.0 (R Core Team 2021). We then visually assessed plots of net-squared displacement by date to identify the distinct plateaus characteristic of resident movements in the non-winter period (Pratt et al. 2017). We calculated the mean dates of transition (if any) between plateaus to separate breeding and summer seasons. The resulting seasonal cutoffs matched other observations of breeding, summer, and winter seasons for sage-grouse in Wyoming (Pratt et al. 2017). We then used these date ranges to approximate seasonal cutoffs that would be biologically relevant for sage-grouse and pronghorn: spring (Apr–Jun; sage-grouse breeding, nesting, and early-brood rearing; pronghorn late gestation and early parturition), summer (Jul–Oct; sage-grouse summer and late-brood rearing; pronghorn late parturition and breeding), and winter (Nov–Mar; non-breeding). We did not delineate unique seasons for feral horses; instead, we evaluated selection of horses relative to each of the aforementioned seasons of co-occurring wildlife species. Based on anecdotal field observations, horses also peaked timing of their late gestation and early parturition in the same time period as pronghorn.

We identified a set of *a priori* land cover, topographical, and distance-to-point variables that hypothetically could influence habitat selection based on our knowledge of the species and study area. We used the National Land Cover Database 2016 shrubland fractional components for the western United States (Rigge et al. 2020) to obtain proportions of each 30-m raster pixel covered by shrubs, sagebrush, or herbaceous plants. We also used this database to obtain mean shrub height per pixel. We used moderate resolution imaging spectroradiometer satellite MOD09Q1 images (8-day temporal and 250-m spatial resolution) to calculate modified soil-adjusted vegetation index (SAVI; Qi et al. 1994). We followed previous methods (Bischof et al. 2012, Merkle et al. 2016) to smooth yearly SAVI time series by first setting all negative values and all pixels classified as clouds, shadow, or snow to null values, flooring the time series of each pixel to a winter (Jan, Feb, Nov, Dec) value (0.025 quantile), replacing all winter null values with this value and filling remaining null values through linear interpolation, and smoothing each time series by applying a 3-scene median filter. We calculated the time-integrated version of this index (iSAVI) to

represent overall vegetation biomass produced during each season (Pettorelli et al. 2005). During the winter season, we used iSAVI calculations from July–October to approximate areas with the greatest residual forage and cover. We calculated mean slope and a topographic wetness index from a 1/3 arc-second digital elevation model (resampled to a 30-m resolution; USGS 2016) using the ArcGIS geomorphometry and gradient toolbox (Evans et al. 2014) within ArcMap 10.6 (Esri, Redlands, CA, USA). We resampled all variables to a 30-m spatial resolution and calculated moving window averages using a 100-m radii to evaluate selection at a local scale that incorporated GPS and land cover error. We also evaluated selection at 500-m and 3,200-m scales for horses and pronghorn because theses distances approximated mean step lengths (500 m) and daily movement distances (3,200 m) for both species. For sage-grouse, we included an additional scale of 6,400 m because previous researchers indicated the importance of this scale to sage-grouse (Walker et al. 2007, Doherty et al. 2016).

We created rasters of Euclidean distances to water sources and oil and gas well pads for each 30-m pixel in our study area. Water sources included excavated reservoirs holding precipitation and runoff, groundwater, stream, or spring-fed reservoirs, and naturally occurring springs (Hennig et al. 2021b). We digitized all water reservoirs from 2017 National Agriculture Imagery Program 1-m aerial imagery (U.S. Department of Agriculture Farm Service Agency 2017) and added known locations of springs provided by the Rawlins BLM Field Office. This dataset represented locations that may have held surface water at some point during the year, but many of these sources do not contain water every year (M. D. Astle, BLM Rawlins Field Office, personal communication). To refine which areas offered surface water during our study period, we calculated the number of revisits per source by horses and pronghorn using the recurse package in R (Bracis et al. 2018). We used a 500-m buffer and an 8-hour lag for this analysis and retained all water sources with >1 revisit. To calculate distances to oil or gas well pads, we used location data from active wells in 2020 (Colorado Oil and Gas Conservation Commission 2020, Wyoming Oil and Gas Conservation Commission 2020). We then calculated a decay function for distance to water and well pad rasters that scaled distance values between 0 and 1, with values increasing closer to a water source or well pad (Buchanan et al. 2014). The decay metric took the form of $e^{-d/a}$, where d was the distance from each pixel to a point source in meters and a was a constant of the following values: 500 m, 1,000 m, 3,200 m, and 6,400 m. We included the 1,000-m scale because extreme variability in these variables at 500 m often resulted in nonsensical parameter estimates. We only used the decay distance to water variable in models of spring and summer habitat selection because surface water was frozen for much of the winter season.

Habitat selection and occurrence overlap

We fit second-order habitat selection (Johnson 1980) models using the glmmTMB package (Brooks et al. 2017) following the framework presented in Muff et al. (2020). For each used location, we randomly generated 10 background points within study area and fit infinitely weighted logistic regression models (Warton and Shepard 2010, Fithian and Hastie 2013) between used and background locations with random intercepts and slopes for each individual (Gillies et al. 2006, Muff et al. 2020). Logistic regression approximates an inhomogeneous Poisson process when the number of background points is sufficiently large (Warton and Shepard 2010). This results in consistent and unbiased parameter estimates and facilitates interpretation as the number of expected presences per unit area (Warton and Shepard 2010, Fithian and Hastie 2013). Incorporating a large number of background points is computationally inefficient, so we weighted each background point with a value of 1,000 while holding all used points to a value of 1 (Muff et al. 2020). We centered and scaled all variables to evaluate the relative strength of selection and for computational efficiency (Schielzeth 2010). Because of the large number of predictor variables and long model run times, we first determined which scale(s) per predictor variable to retain for inclusion in a global model. We used univariate models and retained the scale per variable with the greatest z score. For correlated variables ($|r| > 0.5$), we retained only the variable with the greatest z score. We then fit a full model and dropped variables that were not statistically significant at the $\alpha = 0.05$ level.

We used 5-fold cross validation to assess the predictability of each seasonal model per species (Johnson et al. 2006). We randomly split used locations into 5 independent folds per individual and iteratively re-fit the model by withholding each fold. We then mapped each resulting habitat selection function (HSF) to a 30-m raster clipped to our study area. The HSF took the following form:

$$w_i(x, \beta) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n)$$

where $w_i(x, \beta)$ is the proportional probability of selection, β_n are fixed-effect coefficients, and x_n is the value of a variable at location x. We binned each HSF raster into 10 equal-area quantiles and extracted the binned HSF score (1–10) to locations from the withheld folds. We then implemented a Spearman's rank correlation between the frequency of used points per bin to assess the predictiveness of the model (Boyce et al. 2002).

To assess space use overlap for each species by season combination, we classified the equal-area binned raster into 2 discrete classes: high-use and low-use. We first classified all pixels ≥6 as high-use areas and pixels <6 as low-use areas. We then repeated this process iteratively using 7–10 as the high-use cutoff values. Next, we calculated the percent overlap of high-use areas per species and season by calculating the number of pixels classified as high-use for both species in all pairwise combinations and divided this number by the number of pixels that would represent perfect overlap.

RESULTS

We used location data from 27 female feral horses, 30 female pronghorn, and 45 female sage-grouse (Table 1) to evaluate seasonal habitat selection between 2017–2019 for horses and pronghorn, and between 2018–2021 for sage-grouse. Feral horses selected flatter slopes at the 100-m scale across seasons (Table 2). They also selected lower shrub heights in all seasons, but data supported the greatest support for selection at the 500-m scale in spring and at the 3,200-m scale in summer and winter (Table 2). Horses also selected proximity to water sources within 3,200 m in both spring and summer (Table 2). Pronghorn selected flatter slopes and lower shrub height at the 100-m scale and proximity to water in spring and summer (Table 3). Pronghorn also selected against proximity to oil and gas well pads (3,200-m scale in spring; 1,000-m scale in summer and winter; Table 3). Like horses and pronghorn, sage-grouse selected flatter slopes at the 100-m scale

TABLE 1 Number of used locations per individual per season for evaluation of habitat selection of horses (2017–2019), pronghorn (2017–2019), and greater sage-grouse (2018–2021) in the greater Adobe Town Herd Management Area, Wyoming and Colorado, USA.

Species	Season	Number of individuals	Number of locations
Horse	Spring	27	19,244
Horse	Summer	22	20,338
Horse	Winter	20	24,899
Pronghorn	Spring	27	20,119
Pronghorn	Summer	26	24,951
Pronghorn	Winter	30	34,836
Greater sage-grouse	Spring	24	10,464
Greater sage-grouse	Summer	13	8,171
Greater sage-grouse	Winter	30	11,486

TABLE 2 Standardized beta coefficients and 95% confidence intervals from the final model of third-order habitat selection for feral horses in the greater Adobe Town Herd Management Area, Wyoming and Colorado, USA, 2017–2019.

Variable	Scale	Estimate	LCI	UCI
Spring				
Shrub height	500 m	−0.29	−0.52	−0.06
Slope	100 m	−0.96	−1.39	−0.52
Decay distance to water	3,200 m	0.71	0.46	0.96
Summer				
Shrub height	3,200 m	−0.78	−1.33	−0.23
Slope	100 m	−0.79	−1.10	−0.48
Decay distance to water	3,200 m	0.66	0.43	0.89
Winter				
Shrub height	3,200 m	−0.76	−1.31	−0.21
Slope	100 m	−0.90	−1.37	−0.44

TABLE 3 Standardized beta coefficients and 95% confidence intervals from the final model of third-order habitat selection for pronghorn in the greater Adobe Town Herd Management Area, Wyoming and Colorado, USA, 2017–2019.

Variable	Scale	Estimate	LCI	UCI
Spring				
Shrub height	100 m	−0.33	−0.48	−0.19
Slope	100 m	−0.95	−1.31	−0.60
Decay distance to water	3,200 m	0.56	0.41	0.71
Decay distance to well pad	3,200 m	−0.85	−1.52	−0.18
Summer				
Shrub height	100 m	−0.11	−0.20	−0.01
Slope	100 m	−0.90	−1.32	−0.49
Decay distance to water	3,200 m	0.53	0.34	0.71
Decay distance to well pad	1,000 m	−1.91	−2.79	−1.04
Winter				
Shrub height	100 m	−0.33	−0.45	−0.21
Slope	100 m	−1.76	−2.10	−1.41
Decay distance to well pad	1,000 m	−1.37	−2.18	−0.56

across seasons (Table 4). Sage-grouse selected greater herbaceous cover (100-m scale) and against proximity to well pads in spring (1,000-m scale; Table 4). In summer, sage-grouse selected greater shrub height at the 100-m scale and proximity to water at the 6,400-m scale. Finally, in winter, sage-grouse selected areas with greater vegetation production in summer at the 100-m scale (Table 4).

TABLE 4 Standardized beta coefficients and 95% confidence intervals from the final model of third-order habitat selection for greater sage-grouse in the greater Adobe Town Herd Management Area, Wyoming and Colorado, USA, 2018–2021.

Variable	Scale	Estimate	LCI	UCI
Spring				
Herbaceous cover	100 m	0.63	0.47	0.78
Slope	100 m	−1.69	−2.73	−0.65
Decay distance to well pad	1,000 m	−1.65	−2.63	−0.68
Summer				
Shrub height	100 m	0.41	0.24	0.57
Slope	100 m	−1.24	−2.06	−0.41
Decay distance to water	6,400 m	0.65	0.15	1.15
Winter				
Summer integrated soil-adjusted vegetation index	100 m	1.54	1.37	1.71
Slope	100 m	−1.73	−2.09	−1.37

All models performed well based on Spearman's rank correlations (Figure 2). The mean correlations of the horse HSFs were $r_s = 0.99 \pm 0.01$ (SD), 0.99 ± 0.01, and 0.98 ± 0.01 in spring, summer, and winter, respectively. For pronghorn, the mean correlations of spring, summer, and winter HSFs were $r_s = 0.99 \pm 0.01$, 1.0 ± 0.00, and 0.98 ± 0.02, respectively. For sage-grouse, mean Spearman rank correlations were $r_s = 0.90 \pm 0.03$, 0.98 ± 0.01, and 0.96 ± 0.02 in spring, summer, and winter. Feral horse use was greatest in the western and central portions of the study area in spring and summer and greatest use was in the center of the study area in winter (Figure 3). Pronghorn use was mainly concentrated in the western portion of the study area year-round (Figure 3). Sage-grouse use was greatest in the western and central portions during spring and summer with greater use in the eastern and southern portions in winter (Figure 3). In spring, there was more spatial overlap between areas predicted to be of highest use between feral horses and pronghorn than between horses and sage-grouse (Figure 4). The summer season had the greatest overlap in high-use areas between horses and sage-grouse (Figure 4). Sage-grouse high-use areas were most dissimilar to horse and pronghorn high-use areas in winter (Figure 4). Percent overlap decreased with more restrictive classifications of high-use across pairwise combinations and seasons, but this decrease was sharper for horses and sage-grouse than for horses and pronghorn (Figure 4).

DISCUSSION

Identifying when and where management efforts may be most effective is key to any successful management strategy (Sydenham et al. 2020). Because of limited budgets (Garrot and Oli 2013) and legislative restraints (Scasta et al. 2018), these exercises are increasingly important within feral horse management areas. We evaluated habitat selection of feral horses, pronghorn, and sage-grouse within cold arid steppe and used the results to predict relative probabilities of use and quantify spatial overlap between these species. All species selected flatter slopes across seasons, which led to some level of overlap in high-use areas year-round. Our results indicate that habitat management of feral horses should be linked with pronghorn and sage-grouse management in this area.

The strong degree of spatial overlap between horses and pronghorn reflected similar selection of gentler slopes, lower shrub heights, and proximity to water. Our results match previous studies demonstrating avoidance of
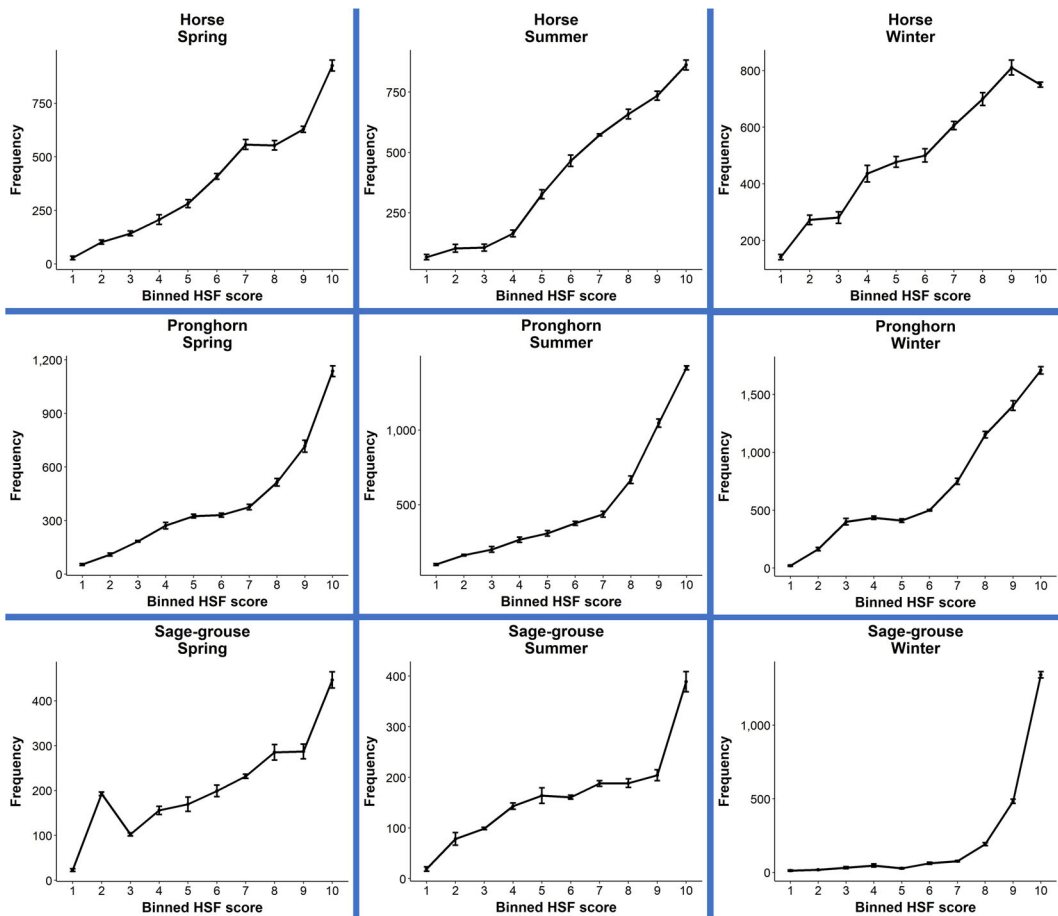
FIGURE 2 Mean (±SD) frequency of withheld used locations per equal-area binned habitat selection function (HSF) score, from a 5-fold cross validation of feral horses (2017–2019), pronghorn (2017–2019), and greater sage-grouse (2018–2021) habitat selection within the greater Adobe Town Herd Management Area, Wyoming and Colorado, USA.

steep slopes (Ganskopp and Vavra 1987, Girard et al. 2013) and that water availability, especially in arid regions, can influence the distribution of both species (Miller 1983, Crane et al. 1997, Mogart et al. 2005). Pronghorn select areas with shorter vegetation (Yoakum 1972), and we documented the same for feral horses. As highly visual animals, pronghorn presumably prefer lower vertical structure to help them detect predators (Yoakum 1972). Shorter structure likely also allows for more freedom of movement, which allows pronghorn to take better advantage of their incredible speed (Yoakum 1981). Horses increase vigilance when presented with novel visual stimuli (Christensen et al. 2005); thus, like pronghorn, they may select shorter vertical structure to improve predator detection and enhance movement.

It remains unknown whether spatial overlap constitutes competition between horses and pronghorn. These species differ in gut morphology (cecal vs. rumen digestion) and feeding strategy (bulk grazer vs. concentrate feeder) so these species may be partitioning forage resources (Schoener 1974, Macandza et al. 2012) with horses selecting graminoids and pronghorn browsing on shrubs (Scasta et al. 2016). In certain systems, however, diet overlap may be higher than expected. Horse diets have been reported to contain >30% browse in harsh winters or in systems with scant herbaceous production (Krysl et al. 1984, Stephenson et al. 1985). Adobe Town is such a
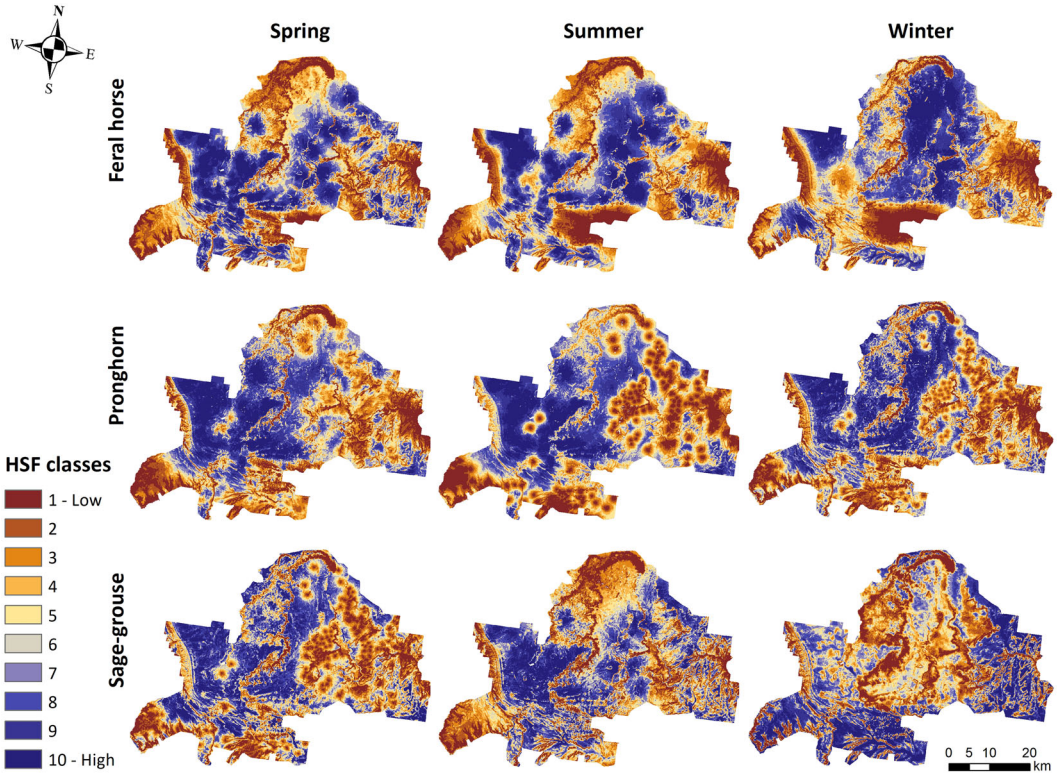
FIGURE 3 Predicted relative probability of use for feral horses (2017–2019), pronghorn (2017–2019), and greater sage-grouse (2018–2021) within the greater Adobe Town Herd Management Area, Wyoming and Colorado, USA. Results of habitat selection functions (HSFs) per species and season were binned into 10 equal-area classifications (each bin is next 10% of probability) with values of 10 indicating areas with the greatest relative probability of use.
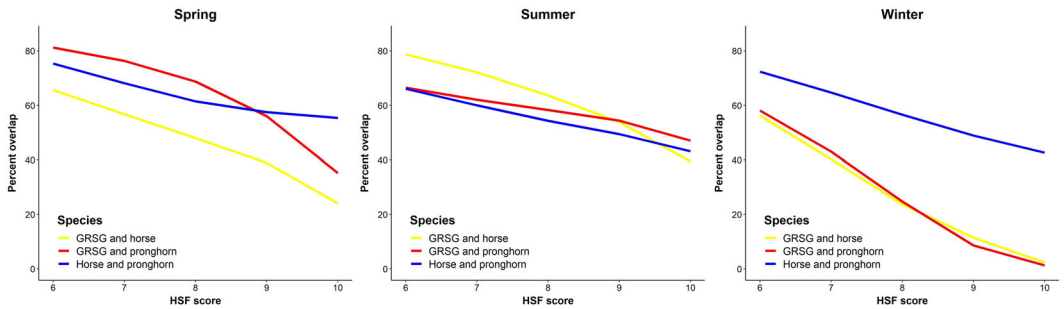
FIGURE 4 Percent spatial overlap of high-use areas between feral horses, pronghorn, and greater sage-grouse (GRSG) in spring, summer, and winter in the greater Adobe Town Herd Management Area, Wyoming and Colorado, USA, 2017–2021. The x-axis represents the areas classified as high-use based on habitat selection function (HSF) binned equal-area quantile scores (6 = bins 6–10, 7 = bins 7–10, 8 = bins 8–10, 9 = bins 9–10, 10 = bin 10). We calculated percent overlap by dividing the number of 30-m raster pixels classified as high-use by both species divided by the number of pixels that would represent perfect overlap of high-use areas.

system, and fecal analyses of horses within this HMA have revealed a high shrub component in their diets (up to 92.5% in winter; M. D. Astle, unpublished report). The WGFD has suspected that competition with horses is a reason why this pronghorn herd has continually failed to meet population targets (WGFD 2017). Consequently, forage competition deserves more investigation given our observation of overlap among high-use areas year-round. Both species also exhibited selection for proximity to water. Horses and pronghorn have similar timing of watering activity (Hennig et al. 2021b), which could lead to interference competition at watering sites (Gooch et al. 2017, Hall et al. 2018), but interference competition between the species may be less of a factor because of the high availability of water in this landscape (Hennig et al. 2021b).

Predicted spatial overlap between horses and sage-grouse was greatest during summer. The overlap during summer was driven by sage-grouse selecting proximity to water. Female sage-grouse raise broods during summer and select areas with increased forb cover and arthropod abundance to provision chicks (Hagen et al. 2007). These resources are commonly found near riparian areas (Crawford et al. 2004), but there are scant riparian areas present in our study area. Horse use is often greater in riparian areas (Crane et al. 1997, Burdick et al. 2021) and their grazing can alter riparian structure (Boyd et al. 2017, Burdick et al. 2021). Controlling access of horses to springs and reservoirs supporting riparian vegetation will benefit late brood-rearing sage-grouse. Sage-grouse were least abundant in our study area during summer, presumably because the area possesses very few riparian areas. Thus, though horse and sage-grouse overlap was greatest during summer, the influence horses have on the larger sage-grouse population of south-central Wyoming may be lowest during summer.

Contrasting with both horses and pronghorn, sage-grouse selected areas with greater herbaceous cover in the breeding season and greater vegetation production during winter. Greater herbaceous cover provides increased nest concealment (Beck and Mitchell 2000, Holloran et al. 2005). In winter, sage-grouse diet is nearly 100% sagebrush (Remington and Braun 1985), so the selection of areas with greater production is likely due to greater forage quantity. We anticipated that horses would also select for greater herbaceous cover or vegetation production because of their dietary preferences for graminoids and their cecal digestion, which necessitates a high-intake strategy (Janis 1976). Shrub height was inversely correlated with both of these metrics, so it appears that lower shrub height is a more important factor for determining second-order habitat selection (Johnson 1980) of horses in this system. A third-order (Johnson 1980) or step-level assessment should be undertaken to better understand habitat selection of feral horses at a finer scale.

The western portion of the study area was predicted to be highly used by horses and sage-grouse during the breeding season. Recent research documented decreased grass height and increased bare ground with greater horse use in the Adobe Town HMA (Hennig et al. 2021a), which could negatively influence recruitment (nest and brood survival) in this sage-grouse population. Further, some of the most well-attended leks fell within areas of high horse use, which may disrupt grouse breeding activity (Muñoz et al. 2021). Sage-grouse were most abundant in the study area during winter, but because the greatest vegetation production occurred at the periphery of the HMA boundary, there was little overlap of high-use areas between horses and sage-grouse during winter. Consequently, concern for horses to negatively affect wintering sage-grouse populations is lower compared to the spring and summer seasons.

By providing evidence of space use overlap between horses, pronghorn, and sage-grouse, we document potential for competitive interactions. This is only one step in the process of understanding the influence that feral horses have on sympatric wildlife. Future research should determine if overlap with horses leads to different behavior choices and decreased fitness of pronghorn, sage-grouse, or both. Fitness consequences are only starting to be evaluated (Coates et al. 2021a), but these will be essential in locales where feral horses overlap sensitive wildlife habitats. Our results mainly apply to the Adobe Town and surrounding HMAs. In areas with greater horse abundance, more homogenous sagebrush cover, or less water availability, such as in the Great Basin, the degree of overlap among these species will likely be different. Therefore, we recommend examining habitat selection and space use overlap between horses and other species of interest in additional BLM Herd Management Areas, USFS Wild Horse and Burro Territories, tribal lands, and other multi-use lands that support feral horse populations.

MANAGEMENT IMPLICATIONS

There is escalating concern for the potential of horses to decrease habitat quality for sympatric wildlife. Proximity to water was selected by horses and sage-grouse during summer, but riparian areas were limited in availability in our study area. To prevent horse-induced habitat alteration of riparian vegetation, we recommend use of wildlife-friendly fencing (smooth bottom wires, >45 cm from ground level) around water sources featuring riparian vegetation to conserve soils and vegetation at these sites yet still allow access by pronghorn and other native ungulates. Further, we stress that keeping horse population sizes within AML is key to limiting horse-related habitat alteration in areas with a high degree of overlap among species. Additionally, AML has not been re-evaluated in light of recent dramatic population increases, so science-based calculations of AML are needed. As horse populations continue to increase, we also recommend regular monitoring of breeding success and winter survival of pronghorn and sage-grouse within horse-occupied areas. If links between horses and decreased fitness of these wildlife species are found, it should warrant more expansive measures of feral horse population control and use restrictions.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

All feral horse handling and use followed protocols approved by the University of Wyoming Institutional Animal Care and Use Committee (protocols 20160826DS00249-01 and 20190802DS00385-01) and at no time were >30 individual horses concurrently equipped with GPS collars, adhering to criteria set forth in the environmental assessment (BLM 2016). We captured and monitored pronghorn and sage-grouse in accordance with protocols approved by the Wyoming Game and Fish Department (Chapter 33 permits: 33-1144, 33-1160, and 33-1303) and University of Wyoming Institutional Animal Care and Use Committee (protocols 20171103DS00295-01, 20170324AP00266, and 20200317JB00413-01).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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