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Temporal Overlap Among Feral Horses, Cattle, and Native Ungulates at Water Sources

JACOB D. HENNIG,[1] *University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, USA*
JEFFREY L. BECK, *University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, USA*
CALEB J. GRAY, *University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, USA*
J. DEREK SCASTA, *University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, USA*

ABSTRACT Feral horse (*Equus ferus caballus*) populations on public rangelands in the western United States threaten forage production for livestock and wildlife habitat. Interference competition between feral horses and heterospecifics at watering sources can have negative effects on livestock and wildlife. Researchers have documented altered timing and behavior of wild ungulates at water sources when horses were present. The few studies examining these interactions have infrequently occurred within areas specifically managed for feral equids and have not occurred in sites with cattle. We used motion-sensitive cameras at 8 watering sources to document watering activity patterns and construct indices of temporal overlap among feral horses, cattle, elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*) within the Adobe Town Herd Management Area in southern Wyoming, USA, between June and September 2018 and 2019. Feral horses, cattle, and pronghorn exhibited a high degree of temporal overlap (>79%) in water use, with feral horses and pronghorn exhibiting the highest estimated percent overlap (88.1%, 95% CI = 86.5–89.6%). Mule deer and elk watering activity also overlapped with horses and cattle but to a lesser degree (<55%). Feral horses spent a mean of 16.7 ± 30.5 (SD) minutes during a watering event and were present at a given water source on average 4.5 ± 6.3% and up to 34.9% of the day, which is less than reported in previous studies. Cattle spent on average 23.5 ± 44.9 minutes during a watering event, and were present on average 4.2 ± 7.7% and up to 42.4% of the day at a single water source. Results of generalized linear mixed-effects models indicated that number of conspecifics was the strongest predictor of visit duration for pronghorn and horses; hour of the day and group size of heterospecifics were informative, but less important, variables. There was no difference in peak visitation time for any species between sites of high versus low horse or cattle use. Despite temporal overlap, we did not find evidence of interference competition between feral horses, cattle, and pronghorn. We recommend future examination of interference competition and its biological consequences between introduced and native ungulates at water sources of varying size across sites, equid population levels, and livestock stocking rates.

KEY WORDS *Antilocapra americana*, cattle, *Cervus canadensis*, elk, *Equus ferus caballus*, feral horse, mule deer, *Odocoileus hemionus*, pronghorn, water sources, Wyoming.

Feral horse (*Equus ferus caballus*) populations on public rangelands in the western United States are rampantly increasing (Scasta et al. 2018), threatening the provision of ecosystem services on multiple-use lands managed by the United States Department of Interior–Bureau of Land Management (BLM) and the United States Department of Agriculture–Forest Service (USFS). Areas with feral horses exhibit decreased plant biomass, altered vegetation composition, and decreased soil stability compared to areas where the species has been excluded or removed (Beever and Herrick 2006, Davies et al. 2014, Boyd et al. 2017), indicating that horses likely alter habitat (e.g., forage availability, escape cover) for wildlife. Beyond habitat alteration, the negative effects of feral horses on wildlife may extend to interference competition between horses and co-occurring species (Perry et al. 2015, Hall et al. 2016, Gooch et al. 2017).

Interference competition constitutes an individual behaviorally mediating the ability of others to use a shared resource (Valeix et al. 2007, Atwood et al. 2011). The potential for interference competition increases when individuals aggregate at a limiting resource (Valeix et al. 2007). Water is a limiting resource in the arid western United States; consequently, sources of water are thought to be sites of potential

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[1] *E-mail: jacobhennig@gmail.com*

interference competition between feral horses and heterospecifics (Perry et al. 2015, Hall et al. 2016, Gooch et al. 2017). Competition between horses and heterospecifics is a management concern (M. D. Astle, BLM, personal communication), especially considering that horses may spend up to 75% of each day at water sources during periods of increased water stress (Perry et al. 2015, Hall et al. 2016). Researchers have documented agonistic behaviors of horses towards elk (*Cervus canadensis*; Perry et al. 2015), and increased pronghorn vigilance (*Antilocapra americana*) when horses are present at watering holes (Gooch et al. 2017). Interference competition from horses has been correlated with shifts in temporal or spatial watering activity patterns of smaller, sympatric species such as pronghorn, mule deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis canadensis*; Ostermann-Kelm et al. 2008, Hall et al. 2018). Such competition can potentially lead to fitness consequences for less aggressive ungulate species, especially as horse populations continue to increase (Gooch et al. 2017).

Despite the influence that feral horses may have on native wildlife at watering sites, the number of studies assessing their effects remains low. To date, no study has documented temporal watering patterns of ungulates within an area explicitly managed for feral horses and cattle. Cattle grazing is a common land use of many BLM Herd Management Areas (HMA), and thus investigation of water use in these areas is important. The addition of cattle to the landscape potentially modifies the degree of interspecific competition because cattle also influence behavior and spatial distributions of smaller species (de Leeuw et al. 2001, Stewart et al. 2002). Conversely, areas supporting cattle grazing may have better water distribution than comparative sites, which could decrease the degree of interspecific competition that native wildlife face.

To our knowledge, no study has examined factors influencing duration of water visits for co-occurring introduced and native species in the United States, but this information could be important in certain rangeland management scenarios. For example, in areas with high potential of interference competition, limiting time spent at water by horses may benefit heterospecifics. On the other hand, if interference competition is already occurring and causing native ungulates to spend more time being vigilant at water sources (Gooch et al. 2017), this may lead to longer visits at water sources and consequently less time devoted to other activities such as foraging, leading to decreased fitness (Lima and Dill 1990).

To understand water activity patterns of ungulates and factors influencing visit duration in an area managed for feral horses and cattle, we employed motion-sensitive cameras at water sources within the BLM Adobe Town Herd Management Area in south-central Wyoming, USA. Our objectives were to describe daily activity water use patterns of all ungulates present in summer within the system, including feral horses, cattle, elk, mule deer, and pronghorn; estimate percent temporal overlap between introduced and native species in daily water use patterns; assess biotic and temporal factors influencing watering visit duration of pronghorn and feral horses; and examine if pronghorn, feral horses, and cattle exhibited altered peak visitation times between sites with high versus low heterospecific use. If interference competition at water sources was present, we predicted longer visit duration times with increased heterospecific group sizes, and significantly different peak arrival times at water sources between sites with high versus low heterospecific use.

STUDY AREA

We conducted our study within the Adobe Town Herd Management Area (ATHMA) located in southern Wyoming (Fig. 1). The ATHMA encompasses 3,413 km^2 and is classified as cold-arid-steppe (Kottek et al. 2006). Across the study area, 30-year normal (1981–2010) mean summer (Jun–Sep) precipitation was 95.6 mm (range = 80.6–121.6 mm) and mean temperature was 16.8°C (range = 15.7–17.3°C; PRISM Climate Group 2004). Summer precipitation was below normal during the years of the study, with mean values of 35.6 mm and 66.3 mm in 2018 and 2019, respectively (PRISM Climate Group 2004). Conversely, mean summer temperatures were higher than normal, with mean values of 18.7°C and 17.5°C in 2018 and 2019, respectively (PRISM Climate Group 2004). Mean elevation was 2,080 m and ranged from 1,883–2,506 m (USGS 2016). Dominant shrub species included big sagebrush (*Artemisia tridentata*), greasewood (*Sarcobatus vermiculatus*), rubber (*Ericameria nauseosa*) and yellow (*Chrysothamnus viscidiflorus*) rabbitbrush, and saltbush species (*Atriplex* spp.). Perennial grass species included cool-season bunchgrasses such as bottlebrush squirreltail (*Elymus elymoides*), prairie Junegrass (*Koeleria macrantha*), and Sandberg bluegrass (*Poa secunda*), along with warm-season grasses such as inland saltgrass (*Distichlis spicata*) and sandhill muhly (*Muhlenbergia pungens*). The BLM set an Appropriate Management Level (AML) for the ATHMA ranging from 610–800 horses; estimated herd size was within AML in 2018 but was 24% above AML in 2019 (BLM 2020). Our study area included 4 cattle grazing allotments, 2 of which allowed grazing from May through November, 1 from March through June, and the other from April through June. Maximum allotted animal unit months (AUM) totaled 5,639 AUM. Our study area also provided priority habitats for game species including elk, mule deer, pronghorn, and greater sage-grouse (*Centrocercus urophasianus*). Oil and natural gas extraction was a predominant use of portions of the ATHMA landscape.

METHODS

We deployed motion-sensitive cameras at watering sources within the ATHMA to record images between June and September 2018 and 2019. We used camera (Stealth Cam IR STC-G30; Stealth Cam, Grand Prairie, TX, USA) units that included a 24-m flash range and 30 infrared emitters set to collect single 4-megapixel images with a 5-second delay. We placed cameras at randomly selected water sources identified from a list provided by the Rawlins, Wyoming, BLM Field Office. This list provided a data set including known and possible sources of water in the study site. We randomly selected sites from the list to place cameras. If a

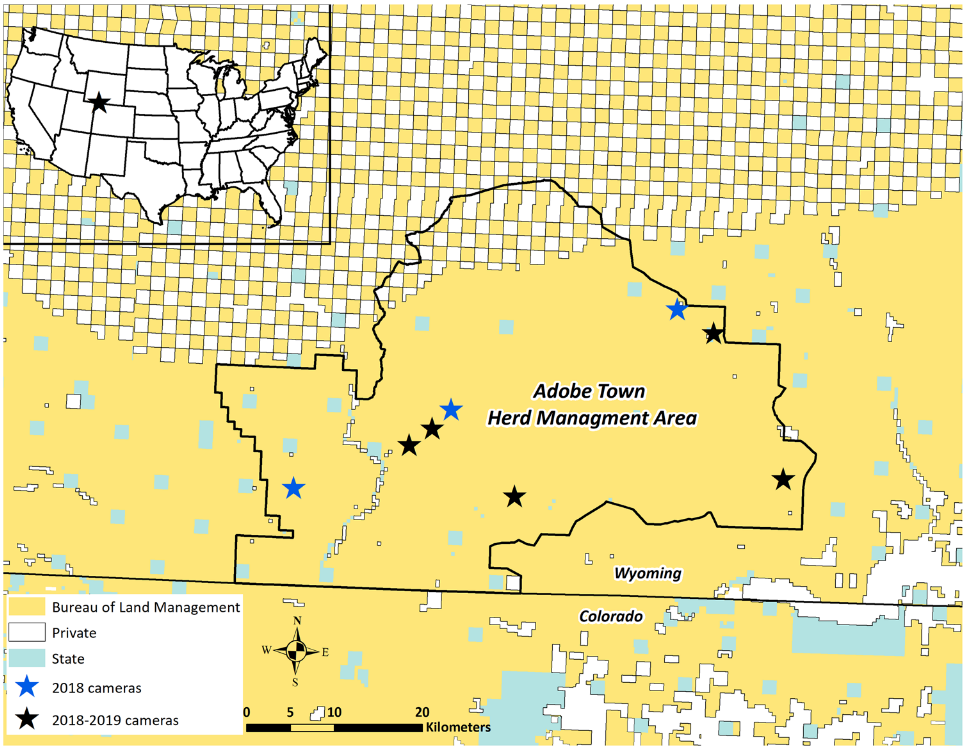

Figure 1. Location and land tenure of the Adobe Town Herd Management Area (ATHMA) in south-central Wyoming, USA, and location of motion-sensitive cameras that recorded images from June through September 2018 and 2019.

selected site did not hold water upon our inspection, we randomly selected another site to place the camera. We set out 11 cameras in 2018, but only 8 provided sufficient data (Fig. 1) and only 5 remained functional after the season because of physical camera damage. In 2019, we randomly selected a subset of camera locations from the 2018 sites to place the remaining 5 working cameras. Water sources included 4 reservoirs holding precipitation and run-off, 2 reservoirs replenished by intermittent streams, and 2 spring-fed reservoirs. Surface area of water sources ranged from 0.03–3.4 ha. We mounted each camera to a steel fence post and positioned them 3–12 m from the water edge and 40–80 cm above ground level. We oriented cameras to capture the near entirety of the water source at small locations (<950 m^2; $n = 4$; Fig. 2A) and the most likely areas of access at larger sites (>1,650 m^2; $n = 4$; Fig. 2B). We used animal track density and observation of animal watering behavior as indicators of water access points. Because data collection did not involve handling or invasive observation of animals, our research protocols described in this paper were exempt from review by the University of Wyoming Institutional Animal Care and Use Committee. We programmed cameras to trigger on both motion and heat, following which they recorded images at 1-minute intervals. We chose 1-minute intervals to maximize battery life and camera storage capacity. We manually processed all images to extract date and time stamps, temperature recordings, and the number of individuals per species present in each image. We included all images in our analyses unless the camera view was moved so that the water source was no longer visible or when all water had evaporated from a site.

Statistical Analysis

To examine water visit duration, we calculated the estimated time of each independent visit by subtracting the timestamp of the first photo from the last photo during each visit. We defined independent watering visits for each

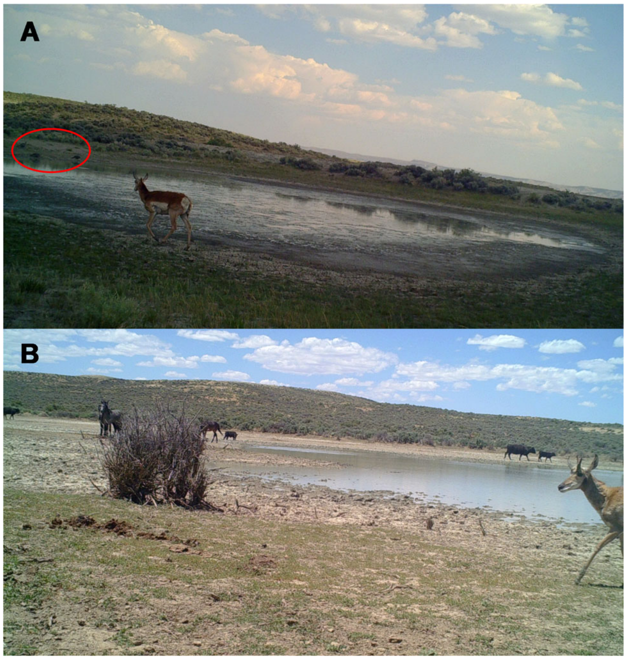

Figure 2. A) Pronghorn and greater sage-grouse (located within red circle) at a small-classified water source and B) feral horses, cattle, and pronghorn at a large-classified water source within the Adobe Town Herd Management Area, Wyoming, USA, June 2018.

species as image sequences separated by ≥30 minutes (Atwood et al. 2011; Hall et al. 2016, 2018). If only 1 photo was triggered during a visit, we estimated the visit to be 1 minute in duration. To estimate percent temporal overlap in daily watering patterns of ungulates within the study area, we used the overlap package (Ridout and Linkie 2009) within Program R (R version 3.6.1, www.r-project.org, accessed 5 Jul 2019). We constructed an observed diel density curve (number of visits per minute of the day divided by number of visits), and then estimated a coefficient of overlap (Weitzman 1970) between both horses and cattle and between each introduced and native species. We then performed a smoothed bootstrap to draw 10,000 randomly simulated observations for estimating 95% confidence intervals around estimates of temporal overlap between ungulate species (Ridout and Linkie 2009).

We used an information-theoretic approach to explore how temporal and biotic variables influence visit duration of pronghorn and feral horses. We modeled visit duration for only pronghorn and feral horses because these were the most commonly recorded species and the only species to be recorded at each site. It was not appropriate to model visit duration of other species with our limited sample size. We modeled visit duration of pronghorn and feral horses with a generalized linear mixed-effects model with a negative binomial distribution using the lme4 package (Bates et al. 2015) in Program R. Temporal variables included day of year, year, and a quadratic term for hour of the day. We included day of year as a covariate to account for decreased water availability as summer progressed. We used a quadratic term of hour of the day as an index for temperature because cameras recorded unrealistic temperatures (>40°C), and a general linear model regressing temperature against the quadratic term of hour of the day was significant ($P < 0.001$). Biotic variables included the maximum number of pronghorn present during a visit, the maximum number of horses present, and the maximum number of cattle present. We included a random effect of camera location in each model and no variables were strongly correlated (i.e., $r > 0.5$). To compare relative importance of each variable, we first centered and standardized each variable (Schielzeth 2010), and then compared all possible variable combinations with a maximum of 3 variables per model. With only 8 water sources, we limited the number of variables per model to avoid overparameterization (Burnham and Anderson 2002). We ranked each model using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002) and model-averaged over the cumulative sum of 0.99 AIC_c weight (w_i) to report beta estimates and 85% confidence intervals of informative variables (Arnold 2010).

We calculated peak arrival time per species per watering location by binning the 24-hour day into 100 equal units and counting the number of independent watering events per unit. We classified the bin with the highest count as peak arrival time. To examine evidence of a temporal shift in peak arrival time at watering sites, we used a Wilcoxon rank sum test to examine if the hour of peak water visitation for a focal ungulate species differed between sites with relative high horse (>3 visits/day; $n = 5$) versus low (<3 visits/day; $n = 3$) use, or sites with cattle use ($n = 5$) versus non-use by cattle ($n = 3$).

RESULTS

We recorded 371 trap days across 8 sites ($\bar{x} = 46.4 \pm 34.2$) in 2018 and 276 trap days across 5 sites ($\bar{x} = 55.2 \pm 41.7$) in 2019. In 2018, 5 water sources evaporated during the sampling period, whereas only 1 evaporated in 2019. We obtained 9,940 photos containing horses, 4,649 with pronghorn, 2,247 with cattle, 328 with mule deer, and 300 with elk. This translated to 1,843, 1,494, 296, 196, and 126 independent visits, respectively. We documented horses and pronghorn visiting all water sources, cattle visiting 5 of 8, mule deer visiting 7 of 8, and elk visiting 4 of 8. Cattle and deer were both present at 3 of 8 sites, cattle and elk at 4 of 8 sites, and deer and elk present at 3 of 8 sites. Cattle had the longest mean visit duration ($\bar{x} = 23.5 \pm 44.9$ min), followed by horses ($\bar{x} = 16.7 \pm 30.5$ min), pronghorn ($\bar{x} = 10.1 \pm 20.3$ min), elk ($\bar{x} = 6.9 \pm 12.9$ min), and mule deer ($\bar{x} = 4.0 \pm 7.8$ min; Fig. 3). On average, water sources were occupied by horses 4.5 ± 6.3% of the day, and up to 34.9% of the day. Cattle were present 4.2 ± 7.7% of the day with a maximum of 42.4%.

Consistent with the natural history of each ungulate species and results of previous research, temporal patterns of feral horse and cattle watering activity overlapped most strongly with pronghorn (Hall et al. 2018; Fig. 4). Feral horses and pronghorn had the greatest estimated overlap in temporal watering activity (88.1%, 95% CI = 86.5–89.6%; Fig. 4A), followed by horses and cattle (83.6%, 95% CI = 81.7–85.5%; Fig. 4B), cattle and pronghorn (78.2%, 95% CI = 76.0–80.4%; Fig. 4C), cattle and elk (68.4%, 95% CI = 63.1–73.5%; Fig. 4D), horses and elk (67.1%, 95% CI = 61.8–72.2%; Fig. 4E), cattle and mule deer (43.2%,

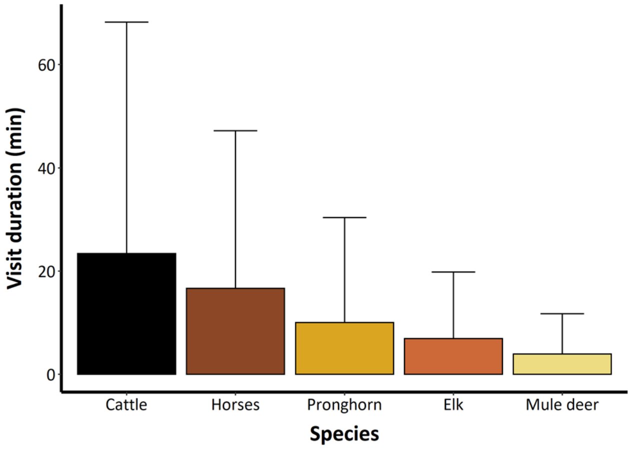

Figure 3. Mean time spent at a watering source ($n = 8$) per watering visit (with SD) per ungulate species within the Adobe Town Herd Management Area, Wyoming, USA, June through September 2018 and 2019.

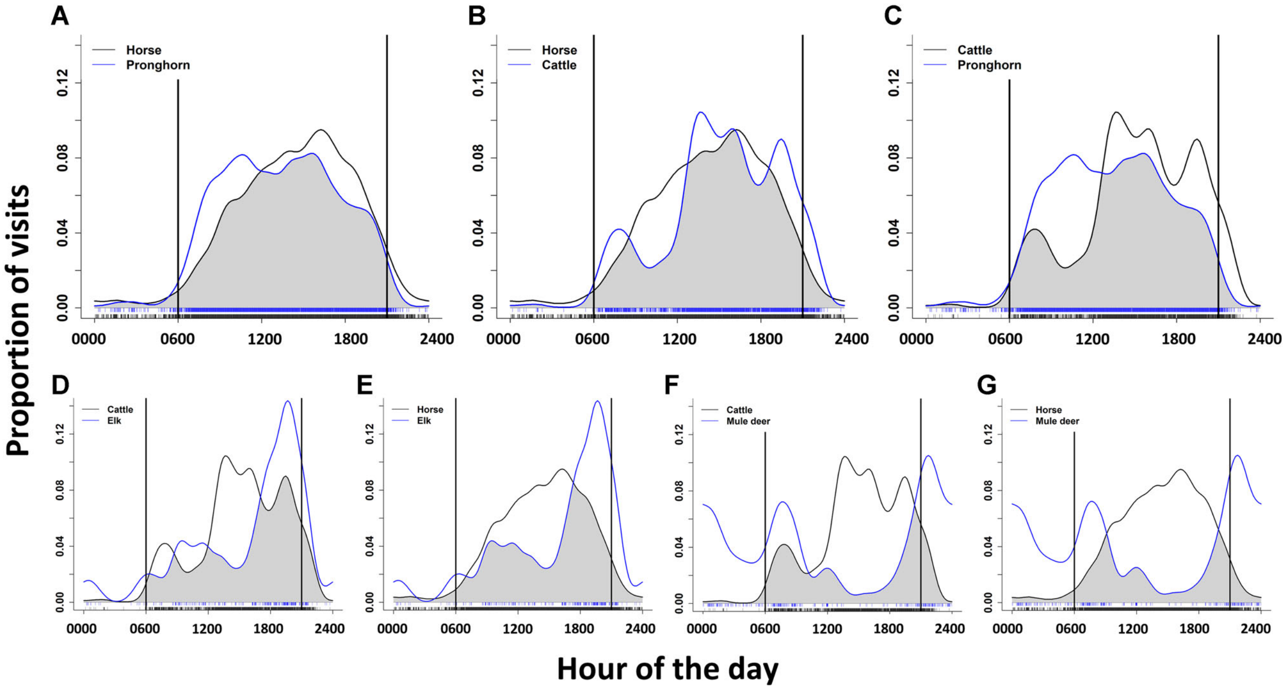

Figure 4. Overlap (shaded region) in temporal distribution of water use by A) feral horses and pronghorn, B) feral horses and cattle, C) cattle and pronghorn, D) cattle and elk, E) horses and elk, F) cattle and mule deer, and G) horses and mule deer in the Adobe Town Herd Management Area, Wyoming, USA, from June through September 2018 and 2019. Rug marks represent the number of independent watering visits per interval and the time between the vertical lines indicates daylight hours. The top 3 frames (A–C) represent the pairwise comparisons with the greatest overlap.

95% CI = 39.0–47.6%; Fig. 4F), and horses and mule deer (37.8%, 95% CI = 33.7–42.0%; Fig. 4G).

Of 1,494 independent pronghorn watering visits, 122 (8.2%) included horses and 19 (1.3%) included cattle. Mean pronghorn group size during visits was 1.5 ± 1.2 (max. = 15). When present during pronghorn visits, mean feral horse group size was 3.6 ± 2.9 (max. = 17) and mean cattle group size was 3.2 ± 3.5 (max. = 13). Five models explaining pronghorn water visit duration received >0 model weight (Table 1). The strongest predictor of pronghorn visit duration was the number of conspecifics present ($\beta = 0.696$, 85% CI = 0.637–0.756). Other informative variables included a significant quadratic effect of hour of the day, with duration peaking at 1200, maximum horse group size ($\beta = 0.112$, 85% CI = 0.066–0.159), day of year ($\beta = 0.112$, 85% CI = 0.052–0.173), and maximum cattle group size ($\beta = 0.091$, 85% CI = 0.045–0.136). Pronghorn visit time was predicted to be 8.7 minutes with 1 cow present and 10.0 minutes with 5 cattle present. Pronghorn visit time was predicted to be 9.1 minutes with 1 horse present and 12.9 minutes with 5 horses present.

Of 1,843 feral horse watering visits, 71 (3.9%) included pronghorn, and 42 (2.3%) included cattle. Mean horse group size during visits was 2.9 ± 2.6 (max. = 23). When present during feral horse visits, mean cattle group size was 2.9 ± 2.3 (max. = 11) and mean pronghorn group size when horses were present was 1.6 ± 1.1 (max. = 7). Five models explaining feral horse water visit duration received >0 model weight (Table 2). The amount of conspecifics present was the strongest predictor of feral horse visit duration

Table 1. Top models explaining pronghorn water visit duration as a function of temporal variables and maximum group size of ungulate species present within the Adobe Town Herd Management Area, Wyoming, USA, June through September 2018 and 2019. Columns represent the number of parameters (K), Akaike's Information Criterion adjusted for small samples sizes (AIC_c), difference between a given model and the top-ranked model ($\Delta\mathrm{AIC}_c$), and model weight (w_i). Only models with >0 model weight and the null model are shown.

Model	K	AIC_c	$\Delta\mathrm{AIC}_c$	w_i
Pronghorn + horse + hour + hour^2	7	9,154.6	0.00	0.65
Pronghorn + cattle + hour + hour^2	7	9,156.4	1.75	0.27
Pronghorn + horse + cattle	6	9,160.0	5.38	0.05
Pronghorn + day + hour + hour^2	7	9,161.9	7.29	0.02
Pronghorn + horse + day	6	9,164.1	9.44	0.01
Null	3	9,579.3	424.72	0.00

Table 2. Top models explaining feral horse water visit duration as a function of temporal variables and maximum group size of ungulate species present within the Adobe Town Herd Management Area, Wyoming, USA, from June through September 2018 and 2019. Columns represent the number of parameters (K), Akaike's Information Criterion adjusted for small samples sizes (AIC_c), difference between a given model and the top-ranked model ($\Delta\mathrm{AIC}_c$), and model weight (w_i). Only models with >0 model weight and the null model are shown.

Model	K	AIC_c	$\Delta\mathrm{AIC}_c$	w_i
Horse + pronghorn + hour + hour^2	7	12,891.2	0.00	0.57
Horse + pronghorn + cattle	6	12,893.4	2.22	0.19
Horse + pronghorn	5	12,894.0	2.86	0.14
Horse + pronghorn + year	6	12,895.8	4.69	0.05
Horse + pronghorn + day	6	12,896.0	4.87	0.05
Null	3	13,580.4	689.23	0.00

($\beta = 0.733$, 85% CI = 0.685–0.782), followed by the maximum pronghorn group size ($\beta = 0.167$, 85% CI = 0.127–0.206), a significant quadratic effect of hour of the day, with duration peaking at 1200, and maximum cattle group size ($\beta = 0.040$, 85% CI = 0.003–0.077). Horse visit duration was predicted to be 12.4 minutes with 1 pronghorn present and 24.2 minutes with 5 pronghorn present. Horse visit duration was predicted to be 10.6 minutes with 1 cow present, and 11.0 minutes with 5 cattle present.

Results of Wilcoxon rank sum tests revealed no significant difference between peak arrival times for pronghorn at sites with high versus low horse use ($W = 10.0$, $P = 0.686$) or cattle use ($W = 8.0$, $P = 0.999$). Similarly, horses exhibited no difference in peak arrival time between sites with and without cattle use ($W = 6.0$, $P = 0.786$), and cattle exhibited no difference in peak arrival time between sites with high versus low horse use ($W = 4.0$, $P = 0.767$).

DISCUSSION

Horses spent less time at water sources within the ATHMA compared to other study areas in the western United States. Perry et al. (2015) reported horses spent an average of 13.6% of the day at their study seep with a maximum of 75.5%. Hall et al. (2016) reported horses spending up to 73.0% of the day at water sources, rendering limited time for other species. The average and maximum observed percentages in our study are less than these values. This suggests that although the ATHMA was classified as arid, water may have been less limiting compared to settings of previous research. The BLM is mandated to manage for feral horses within the ATHMA and water installations are one of the few management tools available to the agency. In the ATHMA, excavated reservoirs holding precipitation and run-off were constructed to spread out distribution of feral horses, whereas groundwater, stream, or spring-fed reservoirs were installed for improving water availability for livestock and native wildlife (M. D. Astle, personal communication). These water developments augmented the few springs and intermittent streams naturally found in the study area and likely increased water availability compared to settings of previous research.

All ungulates inhabiting this system exhibited some degree of temporal overlap in daily watering patterns. Percent overlap was greatest between feral horses, cattle, and pronghorn, an expected result given the natural history of each species and findings of previous research (Hall et al. 2018). These 3 species visited water sources predominantly during diurnal hours compared to mule deer and elk, which visited water more frequently during crepuscular and nocturnal periods. Motion-sensitive cameras may have reduced the capability of capturing animals at night, limiting our inference regarding heterospecific overlap at night. Further, we had a low sample effort and incomplete knowledge of all water locations, so estimated overlap among all species may not be indicative of the entire study area. From the observed degree of overlap, we conclude that pronghorn may be the most susceptible of native ungulates within this system to interference competition from both feral horses and cattle at water; however, the relatively short mean durations of horse and cattle water visits may render any competition insignificant.

Though broad-scale temporal overlap in watering activity was high among pronghorn, cattle, and feral horses, we infrequently observed these species together during the same visit. Our low sample size and incomplete knowledge of water sources within the study area limits our ability to discuss temporal partitioning of water visits, though this should be investigated in future work. At the coarse scale of our investigation, we did not find evidence of different peak visitation time among areas with high and low introduced ungulate use; however, temporal partitioning may be occurring at finer scales, with submissive species waiting until dominant species have left a source. When species were together during a visit, the group size of heterospecifics was correlated with increased visit duration, though not in a 1-sided manner that we predicted (i.e., with greater duration of pronghorn visits, but no effect on equid visits). This may mean that all species face some level of interference competition when the total number of ungulates increases, regardless of species. Our results do not provide any evidence of competition, but we stress that our small sample size may have limited our ability to detect competition.

In our study, sampled water sources were larger than the majority of those from previous studies. Water sources in previous work included springs, seeps, guzzlers, troughs, or overflow ponds (Perry et al. 2015; Hall et al. 2016, 2018; Gooch et al. 2017). More specifically, Hall et al. (2016) reported a mean area of 2.6 m^2 at 23 water sources classified as small, and 1,620 m^2 at 2 larger overflow ponds. Perry et al. (2015) reported a diameter of 15 cm at their study seep during dry spells. The median size of water sources in our study was 1,300 m^2, and all our larger-classified sites (>1,650 m^2; $n = 4$) were greater than the mean of the overflow ponds in Hall et al. (2016). Smaller surface area water sources ostensibly provide limited areas of water access compared to larger sites, thus potentially leading to closer distances between individuals and elevated competition for drinking space (Hall et al. 2016). Indeed, distance from horses is an important variable influencing pronghorn behavior (Gooch et al. 2017). With comparatively larger water body sizes, perhaps it is not surprising that we did not find evidence of interference competition in our study.

Given the limitations of this study (e.g., limited sample size, incomplete knowledge of water sources, and the decreased ability of cameras to capture nocturnal animal visits), our results may not fully represent ungulate watering activity within the entirety of the study area. Nevertheless, the observed temporal overlap in watering activity, especially among feral horses, cattle, and pronghorn indicate that interference competition is a potential issue in the ATHMA. As feral horse populations continue to increase (Scasta et al. 2018) and as future water availability in the western United States is projected to decrease because of climate and anthropogenic changes (Barnett et al. 2008, Cook et al. 2015), an understanding of the fitness consequences from interference competition at water sources will be important. Further, cattle grazing is a common land use practice on BLM and USFS lands, and we need more insight into how horses, cattle, and native wildlife interact at these essential but limited resources. We encourage further research focused on the behavior of ungulates at water sources to determine if interference competition is present (i.e., displacement or increased vigilance of submissive species) and the assessment of fitness consequences resulting from competition.

MANAGEMENT IMPLICATIONS

Our results on temporal overlap suggest there is potential for interference competition between co-occurring feral horses, cattle, and pronghorn at watering sites on western rangelands. To better comprehend the significance of interference competition, future studies should examine behavioral changes and ideally fitness consequences incurred by all species across sites with varying water distribution and population levels of introduced ungulates. This information will aid in identifying specific management actions to lessen the potential deleterious effects of interference competition from introduced ungulates on native wildlife.

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LITERATURE CITED

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Atwood, T. C., T. L. Fry, and B. R. Leland. 2011. Partitioning of anthropogenic watering sites by desert carnivores. Journal of Wildlife Management 75:1609–1615.

Barnett, T. P., D. W. Pierce, H. G. Hidalgo, C. Bonfils, B. D. Santer, T. Das, G. Bala, A. W. Wood, T. Nozawa, A. A. Mirin, et al. 2008. Human-induced changes in the hydrology of the western United States. Science 319:1080–1083.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beever, E. A., and J. E. Herrick. 2006. Effects of feral horses in Great Basin landscapes on soils and ants: direct and indirect mechanisms. Journal of Arid Environments 66:96–112.

Boyd, C. S., K. W. Davies, and G. H. Collins. 2017. Impacts of feral horse use on herbaceous riparian vegetation within a sagebrush steppe ecosystem. Rangeland Ecology and Management 70:411–417.

Bureau of Land Management [BLM]. 2020. Wild horse and burro program data. http://www.blm.gov/programs/wild-horse-and-burro/about-the-program/program-data. Accessed 13 Jul 2020.

Cook, B. I., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances 1:e1400082.

Davies, K. W., G. Collins, and C. S. Boyd. 2014. Effects of feral free-roaming horses on semi-arid rangeland ecosystems: an example from the sagebrush steppe. Ecosphere 5(10):article 127.

de Leeuw, J., M. N. Waweru, O. O. Okello, M. Maloba, P. Nguru, M. Y. Said, H. M. Aligula, I. M. A. Heitkönig, and R. S. Reid. 2001. Distribution and diversity of wildlife in northern Kenya in relation to livestock and permanent water points. Biological Conservation 100:297–306.

Gooch, A. M. J., S. L. Petersen, G. H. Collins, T. S. Smith, B. R. McMillan, and D. L. Eggett. 2017. The impact of feral horses on pronghorn behavior at water sources. Journal of Arid Environments 138:38–43.

Hall, L. K., R. T. Larsen, R. N. Knight, and B. R. McMillan. 2018. Feral horses influence both spatial and temporal patterns of water use by native ungulates in a semi-arid environment. Ecosphere 9(1):e02096.

Hall, L. K., R. T. Larsen, M. D. Westover, C. C. Day, R. N. Knight, and B. R. McMillan. 2016. Influence of exotic horses on the use of water by communities of native wildlife in a semi-arid environment. Journal of Arid Environments 127:100–105.

Kottek, M., J. Greiser, C. Beck, B. Rudolf, and F. Rubel. 2006. World map of the Koppen-Geiger climate classification updated. Meteorologische Zeitschrift 15:259–263.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Ostermann-Kelm, S., E. R. Atwill, E. S. Rubin, M. C. Jorgensen, and W. M. Boyce. 2008. Interactions between feral horses and desert bighorn sheep at water. Journal of Mammalogy 89:459–466.

Penn, C. J., and R. B. Bryant. 2006. Application of phosphorus sorbing materials to streamside cattle loafing areas. Journal of Soil and Water Conservation 61:303–310.

Perry, N. D., P. Morey, and G. S. Miguel. 2015. Dominance of a natural water source by feral horses. Southwestern Naturalist 60:390–393.

PRISM Climate Group. 2020. PRISM climate data. http://prism.oregonstate.edu. Accessed 1 May 2020.

Ridout, M., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322–337.

Scasta, J. D., J. D. Hennig, and J. L. Beck. 2018. Framing contemporary U.S. wild horse and burro management processes in a dynamic ecological, sociological, and political environment. Human-Wildlife Interactions 12:31–45.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1: 103–113.

Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83:229–244.

U.S. Geological Survey [USGS]. 2016. 3DEP products and services: The National Map, 3D Elevation Program Web page. http://nationalmap.gov/3DEP/3dep_prodserv.html. Accessed 14 Mar 2017.

Valeix, M., S. Chamaillé-Jammes, and H. Fritz. 2007. Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. Oecologia 153:739–748.

Weitzman, M. S. 1970. Measure of the overlap of income distribution of white and negro families in the United States. Technical Report 22, U.S. Department of Commerce, Bureau of the Census, Washington, D.C., USA.

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