To the University of Wyoming:

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ABSTRACT

Hennig, J. Feral horse movement, habitat selection, and effects on pronghorn and greater sage-grouse habitat. Ph.D., Department of Ecosystem Science and Management, April 2021.

Increasing populations of feral horses (*Equus ferus caballus*) on western North American rangelands threaten the provisioning of ecosystem services and the stipulation for public lands to be managed for multiple uses. Feral horse grazing can decrease vegetation cover and effect species composition, alter soil structure, and negatively influence faunal communities. Partisan viewpoints regarding the role of feral equids on public rangelands underscore the need for management strategies based on sound science, but information on basic feral horse ecology is limited. Increased understanding of vegetation and soil responses to varying levels of horse use and site-specific information on movement patterns and habitat use are necessary to implement successful management plans. Thus the aim of my dissertation was to increase understanding of feral horse ecology in arid shrublands of western North America and to evaluate the potential for horses to influence habitat quality for co-occurring wildlife species.

I present a broad introduction to my research in Chapter 1, with the following four chapters formatted for journal-specific requirements. In Chapter 2, I conduct a systematic review to record all telemetry-collared wild and feral equids worldwide and evaluate the relative risk of collar-related complications for equids compared to commonly collared North American ungulates, elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*). We found 1,089 collared equids prior to 2017 but while mortality rates for equids were lower than for elk, mule deer, and pronghorn, the lack of sufficient information prevented a critical assessment of relative collar-related complications. Consequently, we encourage explicit reporting of collar-related issues, or lack-thereof, in published literature. This

chapter was published in *Wildlife Research* in 2020 with co-authors J. Scasta, J. Beck, K. Schoenecker, and S. King (Hennig et al. 2020. Systematic review of equids and telemetry collars: implications for deployment and reporting. *Wildlife Research* **47**, 361-371).

Chapter 3 examined the variation in greater sage-grouse (*Centrocercus urophasianus*) habitat quality metrics along a gradient of feral horse use. We found intensity of feral horse use to be an informative predictor of mean grass height and the proportion of bare ground, but other habitat metrics were better explained by topographic and temporal variation. Bare ground linearly increased with increased feral horse use and grass height declined after approximately 638 horse fecal piles/ha. Our results suggest that reductions in feral horse population sizes may limit soil erosion and maintain desired herbaceous structure, but additional management actions are likely needed to sustain high-quality greater sage-grouse habitat. This chapter is in revision at *Journal of Arid Environments* with co-authors J. Beck, C. Duchardt, and J. Scasta.

The objective of Chapter 4 was to understand how differences in digestive morphology and feeding strategy influence the movement syndromes of sympatric ungulates. We found that cecal digesting and bulk roughage feeding feral horses exhibited a more sedentary movement syndrome than ruminating and concentrate selecting pronghorn. Reliance on predictable locations of free-standing water and patches of high vegetation biomass were strong drivers of the more sedentary movements of horses corresponding to their cecal digestion strategy.. Pronghorn unexpectedly showed little selection for relatively unpredictable patches in vegetation green-up, with the lack of need for free-standing water the most likely driver of their relatively nomadic movement. This chapter has been formatted for submission to *Journal of Animal Ecology* with co-authors J. Scasta and J. Beck.

Chapter 5 provides a comparison of seasonal resource selection between co-occurring populations of feral horses, greater sage-grouse, and pronghorn and predicts the proportion of occurrence overlap between the species. Pronghorn have a high proportion of occurrence overlap with horses in both summer (0.84) and winter (0.90), while greater sage-grouse have the highest amount of overlap in the summer season (0.91). Our results suggest that pronghorn face potential competition and habitat alteration from horses year-round, whereas the threat of decreased habitat quality is most prevalent for sage-grouse during later brood-rearing. This chapter has been formatted for submission to *Journal of Wildlife Management* with coauthors J. Scasta, A. Pratt, C. Powell, and J. Beck.

FERAL HORSE MOVEMENT, HABITAT SELECTION, AND EFFECTS ON PRONGHORN AND GREATER SAGE-GROUSE HABITAT IN COLD-ARID-STEPPE

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CHAPTER 1. Introduction

Public rangelands of the western United States provide ecosystem, economic, cultural, and recreational services (Havstad et al. 2007). Rangelands under the jurisdiction of the Bureau of Land Management (BLM) are managed for multiple uses and to ensure sustainability of such services [Federal Land Policy and Management Act 1976 (Public Law 94-579)]. A large quantity (14 million acres) of BLM-managed rangelands provide habitat for feral horses (*Equus ferus caballus*) and burros (*E. asinus*). These equids are protected under the Wild Free-Roaming Horses and Burros Act of 1971 (Public Law 92-195), but burgeoning populations raise concerns regarding the effects that these introduced herbivores have on western rangeland ecosystems (Danvir 2018). Management of feral equids is a complex issue involving competing political, social, economic, and ecological interests.

To fully comprehend this issue, a brief historical overview of horses and burros in the U.S. is helpful. Native North American equids went extinct during the Pleistocene Epoch roughly 10,000 years ago (Grayson 2006). Following this extinction, North America was devoid of equids until introduction of domestic horses by Spanish explorers and pioneers in the late 1400s (McKnight 1959). Through ranchers turning horses out on range and escapes of otherwise domestic stock, feral horse populations eventually proliferated across the western U.S. which now lacked predators due to extinction or eradication (McKnight 1959). This large horse population (estimates range from 2–5 million; McKnight 1959), was integrated into Native American life and became the basis of a successful horse-trading economy until the early 1900s with passage of the Taylor Grazing Act (Flores 2008; Public Law 73-482). This legislation changed western public lands from a ‘commons’ system into livestock grazing allotments. Livestock producers began to view horses as competitors for forage and water and large numbers of horses were killed or removed from public rangelands (Flores 2008). As equid populations dwindled, a concerned public became vocal about protecting the horse and burro populations that they considered American icons (Godfrey and Lawson 1986). Due in part to letter writing campaigns and Hollywood films, the U.S. Congress passed the Wild Free-Roaming Horses and Burros Act in 1971 (Public Law 92-195). This act declared any “unclaimed or unbranded” horse or burro to be “living symbols of the historic and pioneer spirit of the West.” Under threat of fine or imprisonment, the act grants horses and burros protection from “capture, branding, harassment, or death.” It also tasks the BLM and U.S. Forest Service (USFS) to manage equid populations in concert with a ‘natural ecological balance’ using management actions that do not restrict the free-roaming status of horses or burros. The Wild Free-Roaming Horses and Burros Act was so successful in restoring horse and burro populations that legislative action was required to deal with overpopulation issues that compromised federal agencies’ mandate to manage public land for multiple use. The Public Rangelands Improvement Act of 1978 (PRIA; Public Law 95-514) allows for humane removal and adoption of equids in areas where they are above an appropriate management level (AML). However, due to legislative impediments (Scasta et al. 2018) and limited funding (Garrott and Oli 2013), horse and burro populations continue to increase.

Approximately 80,000 horses and 15,000 burros currently roam nearly 14 million ha of BLM-administered public land (BLM 2021). Population estimates are over three times the nationwide maximum AML, while an additional 53,000 equids exist in “off-range” holding facilities, awaiting adoption (BLM 2021). Adoption demand has waned in recent years, confining the animals to spend the remainder of their lives at these facilities as euthanasia or slaughter is not within current BLM policy (NRC 2013). The BLM’s Wild Horse and Burro

Program covers the care-taking bill of these animals, spending approximately $50 million annually, two-thirds of the program's budget (BLM 2021). Cumulative costs of providing for these animals in captivity is projected to surpass $1 billion by 2030 (Garrott and Oli 2013).

Viewpoints on the management of feral horses and burros are extremely partisan, rendering management activities difficult (Wagman and McCurdy 2011, Notzke 2013, Scasta et al. 2018). Management strategies are heavily influenced by public opinion, eliciting a clear need for strategies based on sound science (Nimmo and Miller 2007). Robust quantification of equid movements and resource selection are entirely absent but are needed to understand how these populations interact with their environment. Due to the relatively unrestricted grazing of horses and burros, these introduced equids pose threats to western ecosystems (Nimmo and Miller 2007). Horse grazing can decrease vegetative cover, alter soil structure, and negatively influence co-occurring faunal communities (e.g., Beever et al. 2008, Davies et al. 2014, Hall et al. 2016, Boyd et al. 2017); however, there is little understanding of vegetation and soil responses to varying levels of use, and lack site-specific information on movement patterns and habitat use imperative to successful management strategies.

The purpose of my research is to enhance understanding of feral horse ecology and evaluate potential impacts they may have on shrubland ecosystems. In my second chapter, I present a systematic review of telemetry collar use on wild equids and quantify reporting rate of collar complications. The next chapter explores how greater sage-grouse (*Centrocercus urophasianus*) habitat quality metrics vary along a gradient of horse use (Chapter 3). In my fourth chapter, I use sympatric feral horse and pronghorn (*Antilocapra americana*) populations to understand how differences in ungulate digestion morphology and feeding strategies mediate sedentary versus nomadic movement syndromes. My dissertation concludes with examination of resource selection among feral horses, greater sage-grouse and pronghorn within cold-arid-steppe and quantifies overlap in predicted occurrence between the species across seasons.

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CHAPTER 2. Systematic review of equids and telemetry collars: implications for deployment and reporting

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ABSTRACT

Data from animals equipped with global positioning system (GPS) collars have advanced our understanding of vertebrates, but this technology has rarely been employed to study feral equids. Hesitation to equip feral equids with telemetry collars in the United States is often due to safety concerns which stem from injuries sustained to feral horses (*Equus ferus caballus*) equipped with radio collars in one study from the 1980s. Advancements in collar design over the ensuing quarter-century may have decreased risk of collar-related complications; however, telemetry-based studies on feral equids continue to be limited. We systematically reviewed studies from wild and feral equids worldwide to better understand the mortality and injury risk in application of telemetry collars to equids. Our goals were to: A) report the number of individual equids fitted with telemetry collars (1979–2017), and B) document the number of individual equids that reportedly died or suffered injuries from collars or other sources. We also conducted a comparative review of elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*) to evaluate the relative risk of collar-related complications between equids and routinely collared North American ungulates. We identified 1,089 wild and feral telemetered equids across 48 studies. Of these, 87 (8.0%) were reported to have died, with only 1 (0.09%) mortality attributable to a collar. Comparatively, we found 23.0% (1,095) of 4,761 elk, mule deer, and pronghorn fitted with telemetry collars to have died in the same number of studies, though no mortalities were reported to be related to the collar. While wild and feral equids did not experience increased natural mortality compared to the other ungulates, studies have not provided sufficient information to assess relative risk of collar-related complications. We recommend explicit reporting and discussion of telemetry collar impacts in future publications of all animal species, especially equids, to improve understanding of how telemetry collars may affect study individuals.

INTRODUCTION

In modern wild animal research, global positioning system (GPS) technology is routinely implemented to collect spatiotemporally robust data that can be used to answer questions that could not easily be addressed prior to its development (Cagnacci et al. 2010). By employing GPS technology, we have better understanding of how animals respond to anthropogenic features (e.g., Panzacchi et al. 2013; Sawyer et al. 2013), increased knowledge on habitat selection (e.g., Leclerc et al. 2016; Valls-Fox 2018), and improved information on predator-prey dynamics (e.g., Hebblewhite et al. 2005; DeMars and Boutin). In turn, such information has been imperative for informing successful conservation efforts and evaluating management actions (e.g., Wydeven et al. 2009; Sawyer et al. 2012).

Wild and feral equids are iconic megafauna that are of strong conservation and management concern worldwide. GPS technology has been instrumental in improving the conservation and management of multiple wild equid species. Data from individuals equipped with GPS collars have elucidated movement barriers for Asiatic wild ass (*E. hemionus*; Ito et al.

2013), uncovered unknown migrations of plains zebra (*E. quagga*; Naidoo et al. 2014), revealed that core foraging areas of Grevy's zebra (*E. grevyi*) fell outside of protected ranges (Levikov 2014), and found that desert reintroduction sites represent marginal habitat for the previously extinct-in-the-wild Przewalski's horse (*E. f. przewalskii*; Kaczensky et al. 2008). Contrastingly, GPS technology has rarely been deployed to study feral horses or burros (*E. asinus*), particularly in the United States with safety issues often a concern (Collins et al. 2014; Schoenecker et al. 2020).

The attachment of telemetry transmitters can negatively affect individuals of any species (see Krausman et al. 2004, Walker et al. 2012, Severson et al. 2019). For large, terrestrial mammals, transmitters are often attached to an individual via a neck collar. Equids have been posited to face increased safety risk from neck collars due to their tapering neck shape, which can make for a difficult proper fit (Collins et al. 2014; Schoenecker et al. 2020). These safety concerns are most apparent in the USA, where they led to a moratorium on telemetry collar use (see Schoenecker et al. 2020) on feral horses and burros protected and managed by the federal government under the Wild Free Roaming Horses and Burros Act of 1971 (Public Law 92-195). Recent rapid population growth has led to increased scrutiny of feral horse and burro management amid concerns about effects they may have on native flora and fauna (Scasta et al. 2018). Horse-occupied sites exhibit altered vegetation composition and structure, different faunal communities, and decreased soil integrity compared to similar sites where horses were removed or excluded (Beever and Brussard 2000; Zalba and Cozzani 2004; Beever and Herrick 2006; Davies and Boyd 2019). Further, horses can contribute to spread of invasive species such as cheatgrass (*Bromus tectorum*; King et al. 2019), and negatively influence water use by co-occurring native species (Hall et al. 2016; Gooch et al. 2017). In addition, managers have little, or outdated, information on the natural history of horses and burros, such as home range sizes, daily movement distances, and habitat selection. Data from GPS collars would undoubtedly improve our understanding of these populations, yet safety concerns still cause hesitation to employ this technology.

Complications resulting from feral horse radio-collar studies in the late-1980s are the primary cause of such concerns (NRC 1991). Issues from this Nevada, USA study were primarily attributed to collar design, collar fit, and selection of immature study individuals – all aspects of collar research that have improved over time. Specifically, collars were made of 10.2-cm wide, rigid belting material, which made fine adjustments difficult, and nearly all individuals aged 2–5 years experienced collar complications (NRC 1991). Specific improvements in these areas of collar designs and animal care and use guidelines over the past quarter-century through the integration of better collar material and lighter hardware (such as batteries and GPS units). Furthermore, a recent pilot study illustrated that with proper collar design and fit, GPS collars can be safely used on mature, free-roaming horses (Collins et al. 2014). Nonetheless, the use of GPS collars on federally-protected feral equids in the USA remains a contentious issue that has restricted deployment by researchers to improve ecological understanding and decision making.

To better understand if telemetry collars impose increased risk to equids relative to other wild ungulates, we conducted two literature reviews. We first performed a systematic review of all literature studies reporting telemetry collar data from wild and feral equids from 1979 to 2017. Our goals for this review were to: A) report the number of individual equids fitted with telemetry collars, and B) document the number of individual equids that reportedly died or suffered injuries from collars or other sources. We then conducted a companion abbreviated review with an equivalent number of studies and during the same time period to our equid systematic review to evaluate the relative risk of collar-related complications between equids and routinely collared North American ungulates: elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*). We chose these species because all have been frequently studied with telemetry collars, and each overlap in range with feral equids in western North America (Scasta et al. 2016).

METHODS

We followed systematic review guidelines (Centre for Evidence-Based Conservation 2013) to ensure transparency and repeatability for our global equid review. We defined *a priori* systematic search terms (Table 2.1) and review criteria (Table 2.2) for our review and performed searches using Web of Science and Google Scholar online databases. We assessed each study meeting the review criteria and extracted the following information: (1) study location, (2) telemetry type, (3) number of collared individuals, and (4) number and causes of mortalities and injuries. We included gray literature (reports, theses, dissertations) because their exclusion would have resulted in the loss of valuable information, particularly as it relates to early collaring research on equids in the USA that have never appeared in the peer-reviewed literature (including NRC 1991). While conducting our review, it became apparent that in several instances a single telemetry dataset was the basis for publication of multiple papers. When such situations were identified, we reconciled results to avoid duplication and redundancy in our reported results.

Following our systematic global equid review, we conducted a companion review of studies reporting data from telemetry-collared elk, mule deer, and pronghorn in North America using the Google Scholar database. More than 14,000 studies were found in the initial screening process; thus, we determined that it would be unfeasible to conduct this companion review as an exhaustive review of all studies. We therefore applied analogous search terms (elk OR mule deer OR pronghorn AND collar) but only reviewed 48 studies which corresponded to the number of studies reporting unique telemetry data from equids. We used studies matching the same publication date range and stratification as the systematic global equid review studies (4 studies from 1979–1989, 3 from 1990–1999, and matching years from 1999–2017), and the same number of peer-reviewed articles, reports, and theses/dissertations per year. To accomplish this without imposing bias, we chose which studies to review based on a random number generator. If the resulting study did not meet an appropriate year*publication type, another random study was selected until these criteria were met. We reviewed each study to extract data for the number of collared individuals, along with the number and causes of reported mortalities and injuries occurring during the studies.

RESULTS

Equids

We identified 169 relevant results during our equid review from the screening of titles and abstracts, of which 83 ultimately met our review criteria (Table 2.5). Of these 83 studies, we identified 48 containing unique telemetry datasets (Table 2.3). Collared equids included 4 wild and 2 feral species spanning 18 countries and 5 continents (Fig. 2.1). Species fitted with collars were Asiatic wild ass, Przewalski's horse, plains zebra, Grevy's zebra, feral horse, and feral burro (Table 2.5). We found no sources reporting use of telemetry collars on African wild ass (*E. africanus*), kiang (*E. kiang*), nor mountain zebra (*E. zebra*).

Across all equid species, 1,089 individuals have been fitted with telemetry collars. Of these individuals, 83 (7.6%) were reported as mortalities during studies (Fig. 2.2). Most known mortality causes were natural (old age/disease; 75.9%), followed by depredation (7.2%), hunting/poaching (3.6%), and capture-related mortalities (3.6%). Only one mortality (0.09%); was explicitly stated to be caused by the telemetry collar (NRC 1991). Four causes of mortalities were unknown (4.8%), with no causes reported for an additional 3 deaths (3.6%). Overall, 10 studies (20.8% studies) reported at least a single mortality (Table 2.3), with only one study reporting a death related to a telemetry collar.

Injuries attributed to fit and mass of collars were described in 4 studies (8.3% of studies; NRC 1991; Brooks et al. 2010; Hampson et al. 2011; Fortini 2015), involving 87 individuals (8.0% of collared individuals). Seventy-seven (88.5%) of these injuries were observed in one study in Nevada, USA conducted from 1985–1990 (NRC 1991). Of 336 VHF collars fitted to feral horses in this study in Nevada, 42 were attached too tightly or became too tight over time, resulting in lacerations and infections. Conversely, 35 collars were fitted too loosely or became too loose over time, causing them to slip up over the horses' ears, resulting in cuts, sores, and infections. In addition, reported injuries were explicitly attributed to the placement of collars on immature horses, and the rigid and broad material that was used for the collar (see pages 26-28 in NRC 1991).

In terms of effects that did not cause injury or death, collar weight may have affected the foraging behavior of 5 plains zebra (Brooks et al. 2010). Brooks et al. (2010) fitted 8 collars from 2 different manufacturers to zebra. Subsequently, the 5 individuals fitted with the heavier collar type moved half as much when foraging compared to the 3 individuals wearing lighter collars.

Additionally, 5 feral horses in two studies were reported to have reduced body condition after being affixed with a collar, though causes were unknown (Hampson et al. 2011; Fortini 2015).

North American ungulates

Compared to equids, elk, mule deer, and pronghorn had higher reported mortality across studies. Twenty-seven of 48 (56.3%) studies reviewed (Table 2.4) reported mortalities. In these studies, 4,761 individual elk, mule deer, or pronghorn were fitted with telemetry collars; of these, 1,095 (23.0%) were reported as mortalities (Fig. 2.2). Of those reported, most causes of mortality were either not stated (27.2%) or unknown (18.9%). Hunting or poaching were the most frequent known causes of death (21.5%), followed by depredation (14.8%), natural causes (9.2%), vehicle collisions (5.4%), capture-related mortality (2.6%), and other causes (0.4%). No mortalities were explicitly stated to be collar related. Likewise, no studies mentioned any collar-related injuries or other collar effects.

DISCUSSION

Our review found that equids have been fitted with telemetry collars less frequently than the three species of North American ungulates in this review, both in number of studies and number of individuals collared per study. While safety concerns have prevented telemetry collar use on federally-protected feral equids in the USA, relatively vulnerable population sizes, difficulty of capture, and limited budgets are possible reasons for infrequent use on other equid populations. Nonetheless, vulnerable equid species have been fitted with GPS collars suggesting that safety is either not perceived as an issue for these equids, or the need for collecting spatial data outweighs any potential safety concerns. Different perceptions of zebra, for example, being considered wildlife, compared to feral horses being domesticated, may also have influenced the relative importance and emotive nature of safety against data collection.

Research of wild and feral equids employing GPS collars has provided important insights into their ecology. The ability to collect relocation data at fine spatiotemporal scales assisted in obtaining more accurate estimates of home range sizes and daily movement distances (e.g., Hampson et al. 2010a; Girard et al. 2013; Levikov 2014). Additionally, the resolution of data obtained from GPS enhanced understanding of foraging and movement behaviors of equids at unprecedented scales (Kaczensky et al. 2011a; Owen-Smith et al. 2015). Furthermore, by placing GPS collars on multiple species, we better understand how equids partition resources with sympatric species (e.g., Macandza et al. 2012ab; Owen-Smith and Martin 2015). Better information on all of these topics is sorely needed for improved understanding of how feral equids may impact native flora and fauna and for re-introduced equids in re-wildling or restoration efforts in other countries.

Our review found that the reported mortality rate of collared equids was lower than for collared elk, mule deer, and pronghorn in North America. Some of this disparity is due to native ungulates being routinely hunted; however, removing hunting and poaching mortalities still suggests a higher percentage of these ungulates are killed from other causes than equids (19.0% vs. 7.3%). A major limitation of our review is that mortalities are not required to be reported by publications and often were not reported unless studies were addressing cause-specific mortalities. Many studies that did report mortalities merely mentioned the number of individuals that died, without indicating what caused these deaths. Furthermore, collars may not be retrieved until well after the mortality has occurred, making it difficult to assign a cause of death (e.g., Taylor et al. 2016). Additionally, it is often time and cost-prohibitive to monitor collared animals in the field with enough regularity to identify whether collars have caused injuries to an individual. Many studies employ aircraft to locate individuals or use satellite systems to relay locations, which limits observations of collared individuals after deployment.

Another limitation of our review is that it is difficult to disentangle whether collar complications were a proximate cause of mortality. Injuries or other collar related complications were rarely mentioned in equid studies (4.3% of studies) and completely absent in the ungulate studies we reviewed. We know, however, that collars can cause injuries to ungulates as they caused neck lesions in mule deer and bighorn sheep (*Ovis canadensis*) in California, USA (Krausman et al. 2004). The authors of this study stated they contacted the collar manufacturer to apprise them of the complications from their collars and therefore manufacturers could use the information to design a safer collar. Wild ungulates in North America have been widely studied with telemetry collars for the past half-century, therefore safety issues have likely been identified and corrected so that current safety risk is minimal (e.g., Keister et al. 1988; Diefenbach et al. 2003; Krausman et al. 2004; Obermoller et al. 2018). Because collars have rarely been used on feral equids, information on improving collar design for these animals is lacking. Without more information, we are unable to show whether equids suffer increased risk of mortality or injury due to telemetry collars compared to other ungulates.

CONCLUSIONS

Feral horses are the most abundant equid worldwide (Linnell et al. 2016), yet we know little about their spatial ecology compared to several species of threatened, wild equids. GPS technology could collect robust data useful for improving management of feral horses and burros, especially in countries where debate of their management is contentious (e.g., Australia, Canada, USA). Currently the two federal agencies with authority of equid management in the USA, the United States Department of Interior's Bureau of Land Management (BLM) and the United States Department of Agriculture's Forest Service (USFS) have little information on how animals move across political boundaries, how seasonality influences resource selection and movement patterns, and how these animals compete for or partition resources with wildlife and livestock species.

In the published literature, discussion of collar-related complications, or lack thereof is rare. This is not often a goal of studies; thus, it is seemingly extraneous to include, especially given the cost of page charges. Nonetheless, limited understanding of how telemetry collars impact equids hinders their employment on feral equids under highly scrutinized management. Therefore, we encourage published research to explicitly discuss if collars affected study individuals, especially equids, when applicable.

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TABLES & FIGURES

Table 2.1. Search terms used for the systematic review of wild and feral equid studies utilizing telemetry collars globally to determine safety and application.

Equid term	Technology term
Ass	Collar
Brumby	GPS
Burro	Global Positioning System
Donkey	VHF
Equid	Very High Frequency
Equus	
Grevy’s	
Horse	
Khulan	
Kiang	
Konik	
Mustang	
Onager	
Pony	
Przewalski’s	
Takhi	
Zebra	

Table 2.2. Inclusion criteria for wild and feral equid studies utilizing telemetry collars in a global systematic review to determine safety and application.

Inclusion Category	**Criteria**
Animals	Any species of the genus *Equus* that was either wild or kept in an extensively managed pasture or enclosure
Technology	GPS or VHF telemetry device affixed to a neck collar
Temporal range	1970–2017
Spatial range	Global
Qualifying criteria	We considered studies explicitly employing telemetry tracking devices affixed to a neck collar. We did not include studies that did not report telemetry data, such as papers focused on the capture of animals for subsequent collaring.

Table 2.3. Studies possessing unique telemetry data and meeting *a priori* inclusion criteria in a global systematic review of wild and feral equid studies utilizing telemetry collars (1979–2017). Numbers in parentheses correspond to mortalities and injuries directly attributed to a telemetry collar.

Reference	**Continent**	**Collar Type**	**No. of Collars**	**Publication Type**	**Mortalities Reported**[*a*]	**Injuries Reported**[a]
Feral horse (*Equus caballus*)						
Berman 1991	Australia	VHF	5	Thesis	NA	NA
Hampson et al. 2010a	Australia	GPS	3	Peer-reviewed	0	0
Hampson et al. 2010b	Australia	GPS	12	Peer-reviewed	0	0
Hampson et al. 2011	Australia	GPS	6	Peer-reviewed	3	1 (1)
Fortini 2015	Europe	GPS	6	Thesis	0	4 (4)
Jodowska et al. 2015	Europe	GPS	1	Peer-reviewed	NA	NA
Kohler et al. 2016	Europe	GPS	1	Peer-reviewed	0	NA
Popp and Scheibe 2014	Europe	VHF	1	Peer-reviewed	NA	NA
Radoi et al. 2015	Europe	GPS	32	Peer-reviewed	NA	NA
van Hoesel and van der Werff 2011	Europe	GPS	2	Thesis	0	NA
Collins et al. 2014	North America	GPS	28	Peer-reviewed	0	0
Ehsan et al. 2012	North America	GPS	6	Peer-reviewed	NA	NA
Ganskopp and Vavra 1986	North America	VHF	11	Peer-reviewed	NA	NA
Girard et al. 2013	North America	GPS	4	Peer-reviewed	NA	NA
Goodloe et al. 2000	North America	VHF	10	Peer-reviewed	NA	NA
Leverkus 2015	North America	GPS	13	Thesis	NA	NA
National Research Council 1991	North America	VHF	336	Report	63 (1)	77 (77)
Siniff et al. 1986	North America	VHF	169	Peer-reviewed	4	NA
Zervanos and Keiper 1979	North America	VHF	10	Report	NA	NA
Przewalski's horse (*E. f. przewalskii*)						
Kaczensky and Huber 2010	Asia	GPS	1	Peer-reviewed	0	0
Kaczensky et al. 2008	Asia	GPS	9	Peer-reviewed	1	NA
Kaczensky et al. 2010b	Asia	GPS	5	Peer-reviewed	0	NA
Lugauer 2010	Asia	GPS	2	Thesis	NA	NA
Asiatic wild ass (*E. hemionus*)						
Giotto et al. 2015	Asia	GPS	5	Peer-reviewed	NA	NA
Kaczensky et al. 2008	Asia	GPS	7	Peer-reviewed	1	NA
Kaczensky et al. 2010a	Asia	GPS	16	Peer-reviewed	0	NA
Kaczensky et al. 2010b	Asia	GPS	10	Peer-reviewed	0	NA
Kaczensky et al. 2011a	Asia	GPS	14	Peer-reviewed	1	NA
Kaczensky et al. 2011b	Asia	GPS	12	Peer-reviewed	NA	NA
Shah and Qureshi 2007	Asia	VHF	2	Peer-reviewed	NA	NA
World Bank 2006	Asia	GPS	7	Report	1	NA
Feral burro (*E. asinus*)						
Marshal et al. 2012	North America	VHF	44	Peer-reviewed	NA	NA
Seegmiller and Ohmart 1981	North America	VHF	7	Peer-reviewed	0	NA

Grevy’s zebra (*E. grevyi*)						
Hostens 2009	Africa	GPS	16	Thesis	NA	NA
Levikov 2014	Africa	GPS	26	Thesis	NA	NA
Sundaresan et al. 2007	Africa	VHF	6	Peer-reviewed	NA	NA
Wheeler 2013	Africa	GPS	10	Thesis	NA	NA
Younan 2015	Africa	GPS	21	Thesis	NA	NA
Plains zebra (*E. quagga*)						
Barnier et al. 2014	Africa	GPS	7	Peer-reviewed	NA	NA
Bartlam-Brooks et al. 2011	Africa	GPS	26	Peer-reviewed	2	0
Bradley 2012	Africa	GPS	21	Thesis	4	NA
Brooks 2005	Africa	GPS	25	Thesis	NA	5 (5)
Courbin et al. 2016	Africa	GPS	22	Peer-reviewed	NA	NA
Fischhoff et al. 2007	Africa	GPS	4	Peer-reviewed	NA	NA
Hopcraft et al. 2014	Africa	GPS	13	Peer-reviewed	NA	NA
Kamath et al. 2014	Africa	GPS	70	Peer-reviewed	NA	NA
Macandza 2009	Africa	GPS	6	Thesis	NA	NA
Martin & Owen-Smith 2016	Africa	GPS	4	Peer-reviewed	0	0
Naidoo et al. 2014	Africa	GPS	8	Peer-reviewed	1	NA
Venter et al. 2014	Africa	GPS	7	Peer-reviewed	4	NA

[a] NA means that mortalities or injuries were not reported

Table 2.4. All studies reviewed in the comparative search for studies utilizing telemetry collars on elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*).

Reference	Country	Collar Type	No. of Collars	Publication Type	Mortalities Reported[a]
Elk (*Cervus canadensis*)					
Irwin and Peek 1983	USA	VHF	16	Peer-reviewed	NA
Witmer and deCalesta 1985	USA	VHF	6	Peer-reviewed	NA
Biggs et al. 1997	USA	GPS	6	Report	2
Petersburg et al. 2000	USA	VHF	52	Peer-reviewed	35
DeGroot and Woods 2006	Canada	VHF/GPS	24	Report	1
Sargeant and Oehler 2007	USA	VHF/GPS	175	Peer-reviewed	36
Hebblewhite and Merrill 2007	Canada	VHF/GPS	131	Peer-reviewed	93
Anderson et al. 2008	USA	GPS	7	Peer-reviewed	NA
Gower 2009	USA	VHF	115	Thesis/dissertation	95
Woodside 2010	USA	GPS	10	Thesis/dissertation	0
Laporte et al. 2010	Canada	GPS	22	Peer-reviewed	NA
Smallidge et al. 2010	USA	VHF	110	Peer-reviewed	NA
Brook 2010	Canada	VHF/GPS	130	Peer-reviewed	NA
Baasch et al. 2010	USA	VHF	21	Peer-reviewed	NA
Biggs et al. 2010	USA	GPS	29	Peer-reviewed	NA
Kolada 2011	USA	VHF	10	Thesis/dissertation	0
Webb et al. 2011	USA	VHF/GPS	184	Peer-reviewed	39
Kindall et al. 2011	USA	VHF	156	Peer-reviewed	62
Ciuti et al. 2012	Canada	GPS	122	Peer-reviewed	25
Starr 2013	USA	GPS	10	Thesis/dissertation	1
Beck et al. 2013	USA	VHF	46	Peer-reviewed	7
Monello et al. 2014	USA	VHF	136	Peer-reviewed	29
Pruvot et al. 2014	Canada	GPS	168	Peer-reviewed	NA
Buchanan et al. 2014	USA	VHF/GPS	76	Peer-reviewed	NA
Roberts et al. 2015	USA	GPS	25	Thesis/dissertation	3
Smith 2015	USA	GPS	108	Thesis/dissertation	NA
Mule deer *(Odocoileus hemionus*)					
Springer and Wenger 1981	USA	VHF	23	Report	6
Eberhardt and Caldwell 1983	USA	VHF	17	Peer-reviewed	NA
Relyea et al. 1994	USA	VHF	10	Peer-reviewed	NA
Gray 1995	USA	VHF	77	Thesis/dissertation	24
D-Eon and Serrouya 2005	Canada	GPS	20	Peer-reviewed	NA
Haskell 2007	USA	VHF	303	Thesis/dissertation	135
Bender 2011	USA	VHF	46	Peer-reviewed	22
Kolada 2011	USA	VHF	10	Thesis/dissertation	1
Silbernagel et al. 2011	Canada	GPS	107	Peer-reviewed	NA
McKee 2012	USA	GPS	81	Thesis/dissertation	17
Schuler et al. 2014	USA	GPS	40	Peer-reviewed	2
Northrup et al. 2014	USA	GPS	134	Peer-reviewed	NA
Lendrum et al. 2014	USA	GPS	100	Peer-reviewed	NA

Freeman 2014	USA	VHF	189	Thesis/dissertation	NA
Marescot et al. 2015	USA	GPS	60	Peer-reviewed	24
Coe et al. 2015	USA	GPS	492	Peer-reviewed	162
Mulligan 2015	USA	VHF/GPS	621	Thesis/dissertation	223
Olson et al. 2015	USA	GPS	31	Peer-reviewed	NA
Perez-Solano et al. 2016	Mexico	VHF	9	Peer-reviewed	1
Pronghorn (*Antilocapra americana*)					
Kolar 2009	USA	VHF/GPS	218	Thesis/dissertation	27
Beckmann et al. 2012	USA	GPS	125	Peer-reviewed	NA
Jacques et al. 2014	USA	VHF	61	Peer-reviewed	NA
Collins 2016	USA	GPS	39	Peer-reviewed	2
Taylor et al. 2016	USA	GPS	52	Peer-reviewed	21

[a] NA means that mortalities were not reported

Table 2.5. All studies meeting the review criteria in the systematic search of wild and feral equid studies utilizing telemetry collars.

Reference	Continent	Publication Type	Included in Analyses
Feral horse (*Equus ferus caballus*)			
Berman 1991	Australia	Thesis/Dissertation	Yes
Hampson et al. 2010a	Australia	Peer-reviewed	Yes
Hampson et al. 2010b	Australia	Peer-reviewed	Yes
Hampson et al. 2011	Australia	Peer-reviewed	Yes
Fortini 2015	Europe	Thesis/Dissertation	Yes
Jodowska et al. 2015	Europe	Peer-reviewed	Yes
Kohler et al. 2016	Europe	Peer-reviewed	Yes
Naslund 2016	Europe	Thesis/Dissertation	No
Popp and Scheibe 2014	Europe	Peer-reviewed	Yes
Radoi et al. 2015	Europe	Peer-reviewed	Yes
van Hoesel and van der Werff 2011	Europe	Thesis/Dissertation	Yes
Asa 1999	North America	Peer-reviewed	No
Collins et al. 2014	North America	Peer-reviewed	Yes
Eagle et al. 1992	North America	Peer-reviewed	No
Eagle et al. 1993	North America	Peer-reviewed	No
Ehsan et al. 2012	North America	Peer-reviewed	Yes
Ganskopp and Vavra 1986	North America	Peer-reviewed	Yes
Girard et al. 2013	North America	Peer-reviewed	Yes
Goodloe et al. 2000	North America	Peer-reviewed	Yes
Leverkus 2015	North America	Thesis/Dissertation	Yes
National Research Council 1991	North America	Report	Yes
Siniff et al. 1986	North America	Peer-reviewed	Yes
Zervanos and Keiper 1979	North America	Report	Yes
Przewalski's horse (*Equus ferus przewalskii*)			
Kaczensky and Huber 2010	Asia	Peer-reviewed	Yes
Kaczensky et al. 2008	Asia	Peer-reviewed	Yes
Kaczensky et al. 2010b	Asia	Peer-reviewed	Yes
Lugauer 2010	Asia	Thesis/Dissertation	Yes
Asiatic wild ass (*Equus hemionus*)			
Bayarbaatar 2016	Asia	Thesis/Dissertation	No
Giotto et al. 2015	Asia	Peer-reviewed	Yes
Ito et al. 2013	Asia	Peer-reviewed	No
Kaczensky et al. 2008	Asia	Peer-reviewed	Yes
Kaczensky et al. 2010a	Asia	Peer-reviewed	Yes
Kaczensky et al. 2010b	Asia	Peer-reviewed	Yes
Kaczensky et al. 2011a	Asia	Peer-reviewed	Yes
Kaczensky et al. 2011b	Asia	Peer-reviewed	Yes
Lugauer 2010	Asia	Thesis/Dissertation	No
Nandintsetseg et al. 2016	Asia	Peer-reviewed	No
Shah and Qureshi 2007	Asia	Peer-reviewed	Yes
Sheehy et al. 2010	Asia	Report	No
Sheehy et al. 2012	Asia	Report	No

World Bank 2006	Asia	Report	Yes
Feral burro (*Equus asinus*)			
Marshal et al. 2012	North America	Peer-reviewed	Yes
Seegmiller and Ohmart 1981	North America	Peer-reviewed	Yes
Grevy's zebra (*Equus grevyi*)			
Hostens 2009	Africa	Thesis/Dissertation	Yes
Letoiye 2014	Africa	Peer-reviewed	No
Levikov 2014	Africa	Thesis/Dissertation	Yes
Low et al. 2009	Africa	Peer-reviewed	No
Sundaresan et al. 2007	Africa	Peer-reviewed	Yes
Wheeler 2013	Africa	Thesis/Dissertation	Yes
Younan 2015	Africa	Thesis/Dissertation	Yes
Zero et al. 2013	Africa	Peer-reviewed	No
Plains Zebra (*Equus quagga*)			
Barnier et al. 2014	Africa	Peer-reviewed	Yes
Bartlam-Brooks et al. 2011	Africa	Peer-reviewed	Yes
Bartlam-Brooks et al. 2013a	Africa	Peer-reviewed	No
Bartlam-Brooks et al. 2013b	Africa	Peer-reviewed	No
Bracis and Mueller 2017	Africa	Peer-reviewed	No
Bradley 2012	Africa	Thesis/Dissertation	Yes
Brooks 2005	Africa	Thesis/Dissertation	Yes
Brooks and Harris 2008	Africa	Peer-reviewed	No
Brooks et al. 2008	Africa	Peer-reviewed	No
Cain et al. 2012	Africa	Peer-reviewed	No
Courbin et al. 2016	Africa	Peer-reviewed	Yes
Fischhoff et al. 2007	Africa	Peer-reviewed	Yes
Goodall 2014	Africa	Thesis/Dissertation	No
Hopcraft et al. 2014	Africa	Peer-reviewed	Yes
Kamath et al. 2014	Africa	Peer-reviewed	Yes
Macandza 2009	Africa	Thesis/Dissertation	Yes
Macandza et al. 2012a	Africa	Peer-reviewed	No
Macandza et al. 2012b	Africa	Peer-reviewed	No
Macandza et al. 2013	Africa	Peer-reviewed	No
Martin & Owen-Smith 2016	Africa	Peer-reviewed	Yes
Naidoo et al. 2014	Africa	Peer-reviewed	Yes
Owen-Smith 2013	Africa	Peer-reviewed	No
Owen-Smith and Goodall 2014	Africa	Peer-reviewed	No
Owen-Smith and Martin 2015	Africa	Peer-reviewed	No
Owen-Smith et al. 2012	Africa	Peer-reviewed	No
Owen-Smith et al. 2013	Africa	Peer-reviewed	No
Owen-Smith et al. 2015	Africa	Peer-reviewed	No
Traill et al. 2016	Africa	Peer-reviewed	No
Venter et al. 2014	Africa	Peer-reviewed	Yes
Zhang et al. 2004	Africa	Peer-reviewed	No
Zidon et al. 2017	Africa	Peer-reviewed	No
Zinn 2013	Africa	Thesis/Dissertation	No

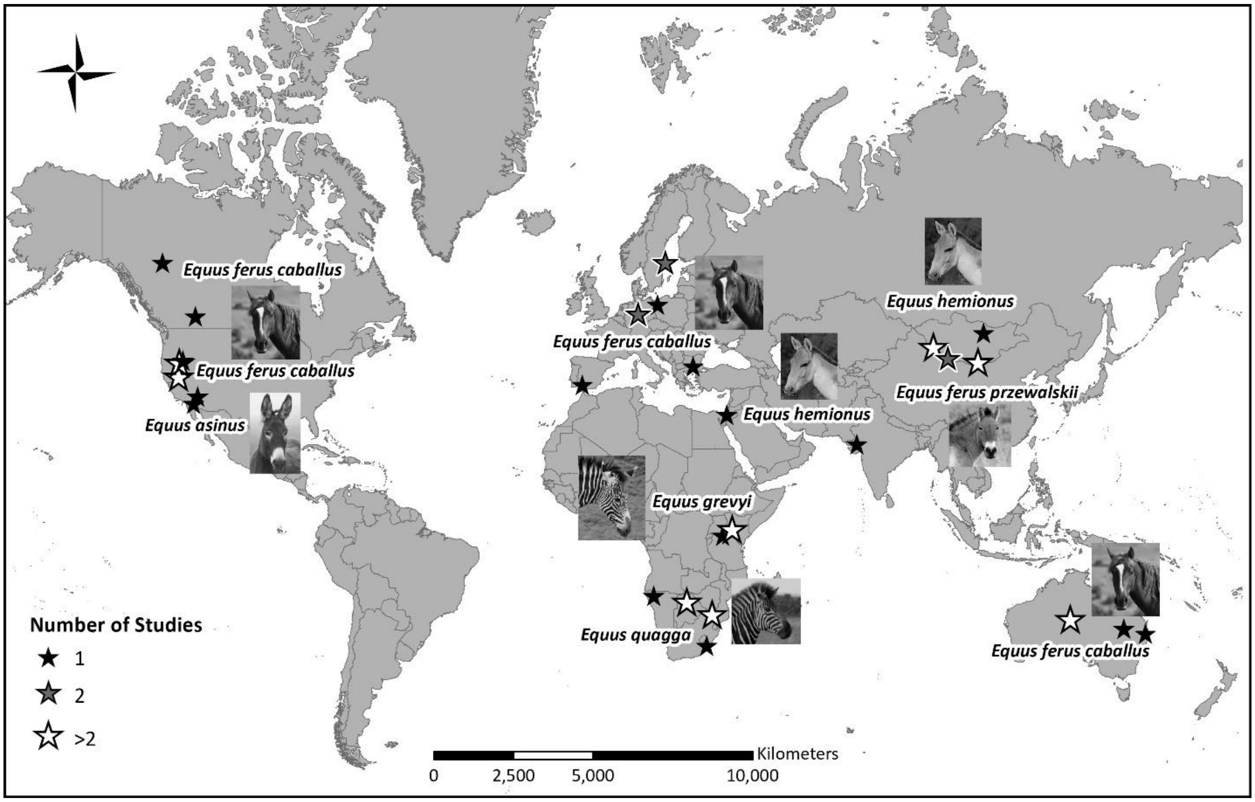

Figure 2.1. Locations of all studies reporting data from telemetered wild and feral equids (1979–2017). Also shown are the number of studies from each location, telemetry collar type (VHF in white, GPS in black), and the species of equids collared at each location. Some studies occurred at more than one location and/or collared more than one equid species.

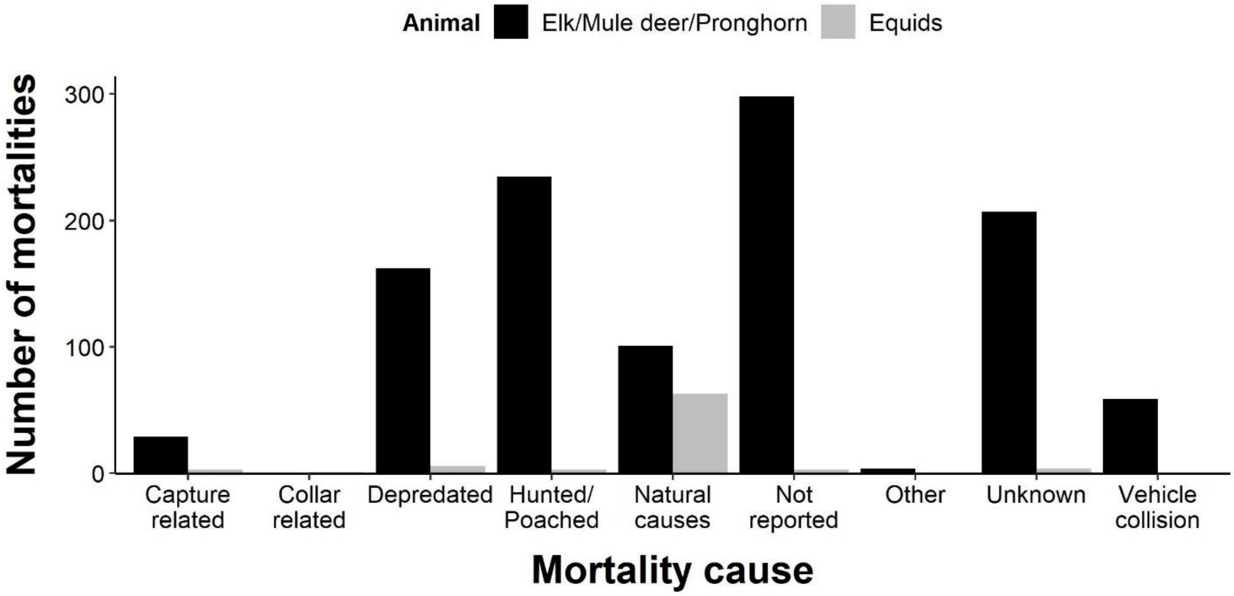

Figure 2.2. Number of all telemetry-collared equids, mule deer, elk, and pronghorn per mortality cause from reviewed studies utilizing telemetry collars (1979–2017).

CHAPTER 3. Variation in sage-grouse habitat quality metrics across a gradient of feral horse use

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ABSTRACT

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

additional management actions regarding feral horse use are needed to sustain high-quality greater sage-grouse habitat.

INTRODUCTION

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

(Scasta et al., 2018) have in part led to the dramatic increase in population sizes of feral horses on Bureau of Land Management land, with recent estimates of 79,568 individuals (BLM 2020). This is >300% of the maximum appropriate management level, a population limit set to maintain a thriving natural ecological balance (Public Law 95-514).

Feral horses alter shrubland structure and composition through consumption, trampling, and as vectors of invasive species spread (Beever and Aldridge, 2011; King et al., 2019). Horse-grazed sites, compared to areas where horses have been removed or excluded, exhibit undesirable rangeland characteristics including lower vegetation biomass and greater soil penetration resistance (Beever et al., 2008; Davies et al., 2014). Mesic areas receive proportionally greater use from feral horses (Crane et al., 1997) and grazing effects in riparian or riparian-adjacent areas have been well-studied (e.g., Beever and Brussard 2000, Boyd et al. 2017). How more xeric upland sites respond to horse use is comparatively understudied; yet, answering this question is critical considering the potential indirect effects on sympatric wildlife (Beever and Aldridge, 2011; Davies et al., 2014).

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

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

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

METHODS

Study Area

We conducted our study within the Adobe Town Herd Management Area located in southern Wyoming, USA (Fig. 1). The management area covers 3,413 km^2 and is classified as cold-arid-steppe (Kottek et al., 2006) with elevation ranging from 1,883–2,506 m (USGS 2016a) and annual mean 30-year normal precipitation and temperatures of 27.7 cm and 6.0°C, respectively (PRISM Climate Group 2004). Dominant shrub species included Wyoming big sagebrush (*Artemisia tridentata* Nutt. *Wyomingensis* Beetle & Young), greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.), yellow rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), rubber rabbitbrush (*Ericameria nauseosa* (Pall. ex Pursch) G.L. Nesom & Baird), and assorted saltbush species (*Atriplex* spp.). Perennial grass species included cool-season (C3 photosynthetic pathway) bunchgrasses such as squirreltail (*Elymus elymoides* (Raf.) Swezey), prairie Junegrass (*Koeleria macrantha* (Ledeb.) Schult.), and Sandberg’s bluegrass (*Poa secunda* J. Presl), along with warm-season (C4 photosynthetic pathway) grasses such as inland saltgrass (*Distichlis spicata* (L.) Greene), and sandhill muhly (*Muhlenbergia pungens* Thurb.). Cheatgrass was the main exotic annual grass present. Estimated herd size was within appropriate management level (610–800 horses) in 2018 but was 24% above appropriate management level in 2019, the years of our study (BLM 2020). Our study area included six livestock allotments permitted for summer grazing by cattle (*Bos taurus*). Allotted animal unit months between March and November totaled 6,596. The study area provided crucial habitat for iconic wildlife species including sage-grouse, elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*).

Horse use and field data collection

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

Using horse location data beginning on 1 May each year, we constructed utilization distributions for horse groups (bands) containing a GPS-collared individual using dynamic Brownian Bridge movement models (Kranstauber et al., 2012). Horses form static social groups and therefore the locations of one individual reflect locations of the entire group. During the 2018 data collection period, 18 unique horse bands featured a collared individual compared to 15 bands in 2019. We divided each utilization distribution into strata based on levels of predicted use: high (top 10% of use), moderately high (>10-25%), moderately low (>25-50%), and low (>50%). For each horse by stratum combination, we randomly selected a sample location used by the horse within the previous 2 weeks. We constrained sampling availability to sagebrush habitat defined by LANDFIRE Existing Vegetation Type 1.4 (USGS 2016b) and aimed to lessen topographic influence by constraining sample sites to fall within one standard deviation of the mean slope, elevation, and compound topographic index of the study area. After completing one round of field data collection, we updated utilization distributions with newly acquired location data and repeated the sample selection process. We ensured that samples were evenly distributed across each horse band by utilization distribution combination by sampling one location per utilization distribution level per band per year.

At each sample location we measured variables known to influence habitat quality for sage-grouse (Table 1). To quantify vegetation structure and composition at each sampling location, we established four perpendicular 50-m transects oriented along each cardinal direction. We measured percent shrub canopy cover and gap length between shrubs using the line-intercept method (Canfield 1941). We assessed sagebrush height by measuring the maximum height of the plant at the center location and along each transect at 5, 15, 25, 35, and 45 m intervals ($n = 21$). We recorded visual obstruction readings using a Robel pole (Robel et al., 1970) and quantified vegetation composition using 0.5 m^2 (100 cm x 50 cm) Daubenmire quadrats (Daubenmire, 1959) at the same intervals. Within each Daubenmire quadrat we estimated canopy cover of the following 13 plant functional groups and ground cover classes: cheatgrass, native annual grasses, native perennial C3 grasses, and native perennial C4 grasses, sedges, forbs, cacti, shrubs, litter, bare ground, lichen, biological soil crust, and rocks; via the following cover classes: 0, <1%, 1–5%, 6–25%, 51–75%, 76–95%, >96% (Scasta et al., 2016). To increase estimation accuracy, we taped sections of the quadrat to signify polygons representing 5% and 25% of the quadrat area. We recorded the droop height of the tallest grass specimen present within the 5% polygon to assess grass height (Connelly et al., 2003).

Ungulate fecal counts can be a useful metric for intensity of use and is relatively easy for managers and researchers to employ (Forsyth et al., 2007). To determine if utilization distribution levels were a similarly effective predictor of horse use, we counted individual fecal piles for horses within 2 m along both sides of each of the four, 50-m perpendicular transects

(800 m^2; Beever and Brussard 2004). Male horses defecate in latrines, which make counting these piles difficult; thus, we did not include such piles in our counts (Street 2020). To account for use by cattle and wild ungulates (elk, mule deer, and pronghorn), we counted fecal piles for these species as well. Species-specific identification of native ungulate feces was difficult to universally apply, therefore counts for these native ungulates were pooled together and analyzed collectively.

Spatial data

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

Statistical analyses

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

Burnham and Anderson 2002) and used the top ranked variable as our metric of horse use in the following analyses.

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

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

RESULTS

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

Horse use appeared in highly ranked models explaining variation in percent bare ground and grass height (Table 2). Bare ground increased with horse use ($\beta = 0.11$, SE = 0.04; Fig. 3A) and as the summer progressed ($\beta = 0.16$, SE = 0.04), but declined with steeper slopes ($\beta = -1.40$, SE = 1.09) and higher elevations ($\beta = -0.05$, SE = 0.02; Table 3). A quadratic term of horse use explained grass height better than the linear term (Table 2). Grass height declined after approximately 638 horse fecal piles/ha (Fig. 3B) and was higher in 2019 than 2018 ($\beta = 2.07$, SE = 0.46; Table 3). Horse use was not informative for explaining variation in any other habitat metric (Table 3). Perennial grass cover was higher in 2019 than 2018 ($\beta = -0.03$, SE = 0.01) and increased with elevation ($\beta = 0.02$, SE = 0.01). Cheatgrass cover declined with both elevation ($\beta = -0.03$, SE = 0.01) and percent silt at the 5–15 cm depth ($\beta = -0.23$, SE = 0.04). Shrub height increased with percent sand at the 5–15 cm depth ($\beta = 0.12$, SE = 0.05), but declined with higher elevations ($\beta = -0.04$, SE = 0.02), and decreased with native ungulate use ($\beta = -0.10$, SE = 0.03). Maximum shrub intercept length was also negatively associated with native ungulate use ($\beta = -0.66$, SE = 0.19; Table 3). No measured variables were informative predictors of visual obstruction or shrub cover (Table 3).

DISCUSSION

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

The link between increased horse use and percent bare ground is troubling because a high proportion of bare ground is an indicator of poor soil quality and subsequently rangeland health (Derner et al., 2018; Pyke et al., 2002). Without protection from vegetation and litter, exposed areas of bare ground are prone to increased soil erosion and exotic plant invasion (Davies and Boyd, 2019). Increased runoff and sediment loss from erosion reduces water and nutrient availability for plant growth and propagation (Rostagno et al., 1991). This often leads to decreased vegetation production and may also result in unwanted state changes (Chartier and Rostagno, 2006; Pimentel et al., 1995). Though we did not find a link between horse use and cheatgrass cover, bare ground is highly susceptible to cheatgrass invasion (Jessop and Anderson, 2007). Cheatgrass establishment is a major threat to western US rangelands because it leads to decreased plant diversity, altered herbaceous structure, and increased fire frequency, all of which combine to reduce sage-grouse habitat quality (Connelly et al., 2004; Knapp, 1996, Lockyer et al. 2015).

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

Differences in vegetation height between areas with and without feral horse grazing have been documented in several systems (Beever and Brussard, 2000; Boyd et al., 2017; Eldridge et al., 2019). Here we present a threshold response of grass height to a gradient horse use. We detected this threshold response because the quadratic term for horse use was a better fit than the linear term. We acknowledge that grass height only minimally declined at greater use levels; nonetheless, this result has important implications to sage-grouse habitat quality as taller grass provides better nest concealment and cover for chicks (Beck and Mitchell, 2000; Doherty et al., 2014; Hagen et al., 2007; Holloran et al., 2005). It is critical to note that we measured grass height during June and July following the peak nesting period for sage-grouse (Schroeder et al., 2020); thus, our results are most applicable to understanding the potential for horses to negatively influence brood-rearing habitat. Furthermore, advanced phenological expression of grasses during our sampling period ensured shorter grasses at sampling locations were not merely a factor of measuring them before they reached their potential height, which has led to spurious results in past models of sage-grouse nest success (Gibson et al., 2016; Smith et al., 2018).

We attribute the responses of bare ground and grass height to anatomical differences between horses and co-occurring ungulates. Unlike native ungulates and cattle, horses possess upper incisors (Janis, 1976). This adaptation allows them to clip vegetation closer to the ground than sympatric species, which can affect the ability for vegetation to regrow following herbivory (Menard et al., 2002; Symanski, 1994). Horses are also larger-bodied than native herbivores and frequent use by these relatively large animals (>400 kg: Berger 1986) can increase soil compaction (Beever and Herrick, 2006), further hindering plant growth (Kozlowski, 1999).

Fecal piles have frequently been used as an index of relative ungulate use (Forsyth et al., 2007; Goda et al., 2008; Rhodes et al., 2017, Street 2020). Because we concurrently had GPS-collared horses with 2-way Iridium-based technology, we were able to assess the efficacy of near-real time horse data in assessing cumulative population use. Fecal piles did not significantly vary among the four utilization distribution levels and while this may seem surprising given the call for more fine-scale movement data to improve our understanding of habitat use (Cagnacci et al., 2010), there are several reasons why individual utilization distributions were uninformative in our experiment. First, 4 to 12 weeks of GPS data (336 to 1008 locations assuming a 2-hour fix rate) may not be a sufficient sample size to properly estimate and differentiate between use levels. Second, we observed a wide range in the number of individuals per horse band (2–15, unpublished data) and many other bands without a collared individual. Fecal pile counts capture the increased use of larger bands of horses and horse bands without collared individuals, whereas utilization distribution levels only reflect the collared individuals. Subsequently, because horses exhibited non-exclusive home ranges, utilization distribution levels of one band do not account for additional use of another. Without knowing the movements and group sizes for each band in the study area, we could not appropriately correct utilization distribution levels; thus, the number of fecal piles per sample location was a better metric of total horse use.

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

CONCLUSIONS

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

94-579). Manipulation of when and where horses graze, in addition to population management, is recommended to sustain wildlife habitat quality within herd management areas into the future.

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TABLES & FIGURES

Table 3.1. The set of sagebrush habitat quality metrics measured across a gradient of feral horse (*Equus ferus caballus*) use, along with their importance to greater sage-grouse (*Centrocercus urophasianus*) and predicted response of each metric from increased horse use, Adobe Town Herd Management Area, Wyoming, USA, June through August 2018–2019.

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

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

Table 3.2. Candidate models for explaining variation in sagebrush habitat metrics across a gradient of feral horse (*Equus ferus caballus*) use within the Adobe Town Herd Management Area, Wyoming, USA, from June through August 2018–2019. Models <2 AIC_c of top model are shown, in addition to the null model.

Model	**K**	**AIC_c**	**ΔAIC_c**	**w_i**
Bare ground cover				
Horse + Elevation + Day + Slope	6	978.3	0.00	0.12
Horse + Elevation + Day + Slope + Ungulate	7	978.3	0.03	0.12
Horse + Elevation + Day + Slope + Silt [a]	7	978.8	0.54	0.09
Horse + Elevation + Day + Slope + Ungulate + Silt [a]	8	979.3	1.03	0.07
Horse + Elevation + Day + Silt [a]	6	979.3	1.04	0.07
Horse + Elevation + Day + Slope + Ungulate + Cattle	8	980.1	1.77	0.05
Horse + Elevation + Day	5	980.1	1.84	0.05
Null	3	1011.8	30.48	0.00
Native perennial grass cover				
Elevation + Day + Year + Ungulate	7	-318.4	0.00	0.33
Elevation + Day + Year + Ungulate + Cattle	8	-317.3	1.11	0.19
Null	3	-292.1	26.34	0.00
Cheatgrass cover				
Silt [a] + CTI + Elevation + Latitude + Longitude	7	-393.5	0.00	0.50
Silt [a] + CTI + Elevation + Aspect + Latitude + Longitude	8	-393.4	0.16	0.46
Null	5	-336.3	57.22	0.00
Grass height				
Aspect + Year + Latitude + Longitude	6	633.1	0.00	0.25
Year + Horse + $Horse^2$ + Latitude + Longitude	7	633.3	0.23	0.23
Year + Latitude + Longitude	5	633.5	0.37	0.21
Aspect + Year + Horse + $Horse^2$ + Latitude + Longitude	8	634.1	0.98	0.16
Null	4	646.3	13.17	0.00
Visual obstruction				
Ungulate	4	226.2	0.00	0.94

Null	3	231.8	5.53	0.06
Shrub cover				
Ungulate	3	-373.9	0.00	0.23
Ungulate + Aspect	4	-373.3	0.57	0.17
Ungulate + Cattle	4	-372.1	1.74	0.10
Ungulate + Horse	4	-372.0	1.87	0.09
Null	2	-371.6	2.26	0.07
Shrub height				
Elevation + Sand [a] + Ungulate	6	948.1	0.00	0.57
Null	3	969.8	21.73	0.00
Maximum shrub intercept length				
Ungulate	3	1459.1	0.00	0.32
Ungulate + Slope	4	1459.3	0.17	0.29
Ungulate + Year	4	1460.0	0.91	0.20
Ungulate + Slope + Year	5	1460.2	1.07	0.19
Null	2	1469.9	10.75	0.00

[a] 5–15 cm depth

Table 3.3. Model-averaged parameter estimates, standard errors, and 85% confidence intervals for informative variables explaining variation in sagebrush habitat metrics across a gradient of feral horse (*Equus ferus caballus*) use within the Adobe Town Herd Management Area, Wyoming, USA, from June through August 2018–2019.

Parameter	**Estimate**	**SE**	**85% CIs**
Bare ground			
Intercept	121.44	31.40	(76.39, 166.49)
Slope	-1.40	1.09	(-3.10, -4.47)
Day	0.16	0.04	(0.10, 0.22)
Horse	0.11	0.04	(0.04, 0.19)
Elevation	-0.05	0.02	(-0.07, -0.02)
Native perennial grass cover			
Intercept	-3.62	2.29	(-6.92, -0.33)
Rho [a]	0.39	0.10	(0.24, 0.54)
Year2019	-0.28	0.11	(-0.45, -0.12)
Exotic annual grass cover			
Intercept	8.51	1.59	(5.38, 11.64)
CTI	-0.07	0.03	(-0.12, -0.01)
Grass height			
Intercept	-48.75	29.95	(9.35, 13.26)
Year2019	1.85	0.48	(1.43, 2.77)
Horse	0.03	0.05	(0.02, 0.14)
Horse^2	-0.00	0.00	(-0.00, -0.00)
Visual obstruction			
Intercept	1.76	0.30	(1.33, 2.20)
Rho [a]	0.30	0.12	(0.12, 0.47)
Shrub cover			
Intercept	0.17	0.01	(0.15, 0.19)

Shrub height			
Intercept	117.79	35.82	(66.23, 169.35)
Rho [a]	0.21	0.13	(0.03, 0.39)
Sand [c]	0.12	0.05	(0.05, 0.19)
Ungulate	-0.10	0.03	(-0.15, -0.06)
Elevation	-0.04	0.02	(-0.07, -0.02)
Maximum shrub intercept length			
Intercept	163.21	14.85	(141.88, 184.54)
Ungulate	-0.66	0.19	(-0.94, -0.39)

[a] spatial autoregressive parameter

[b] simultaneous autoregressive error coefficient

[c] 5–15 cm depth

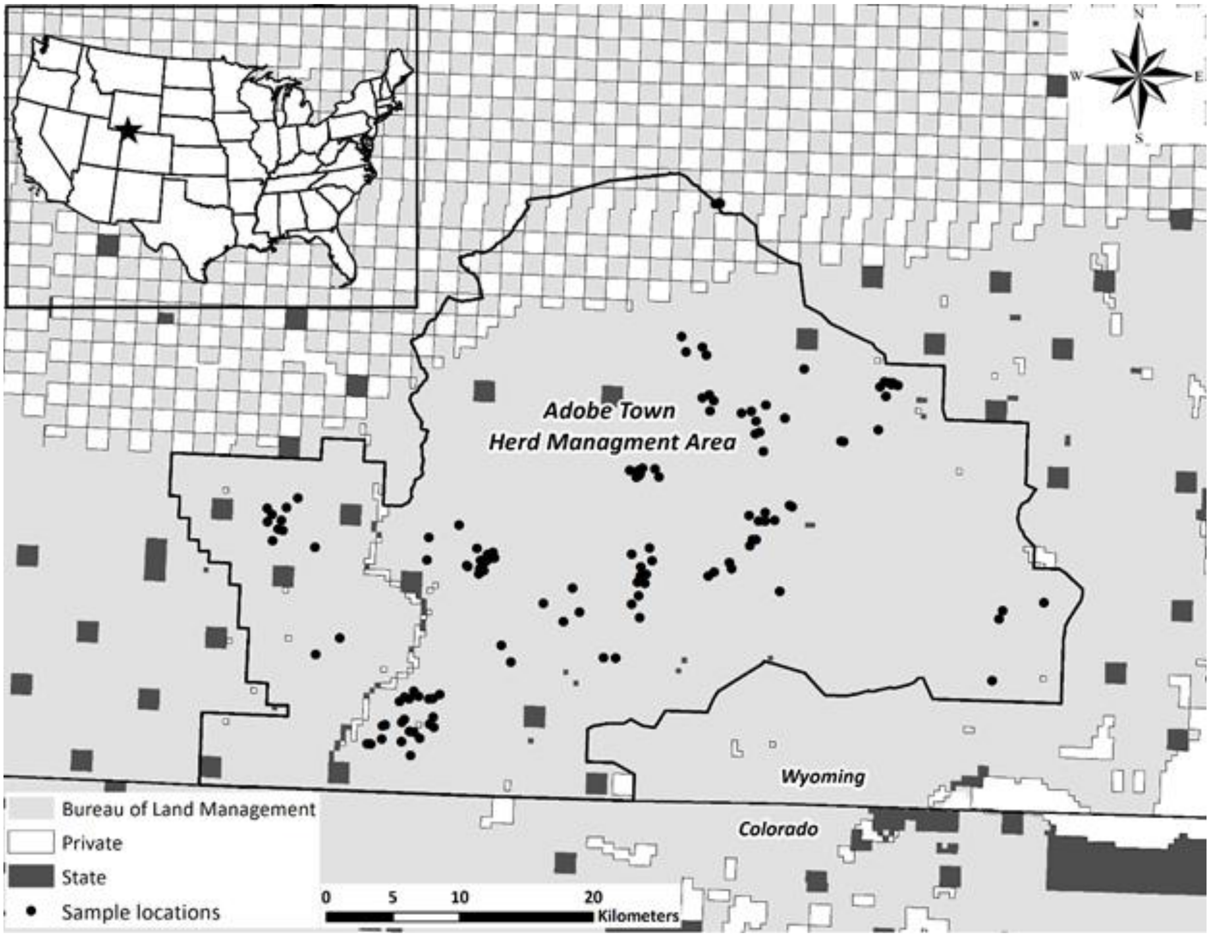

Figure 3.1. Sample locations and land surface ownership within the Adobe Town Herd Management Area in south-central Wyoming, USA, June through August 2018–2019.

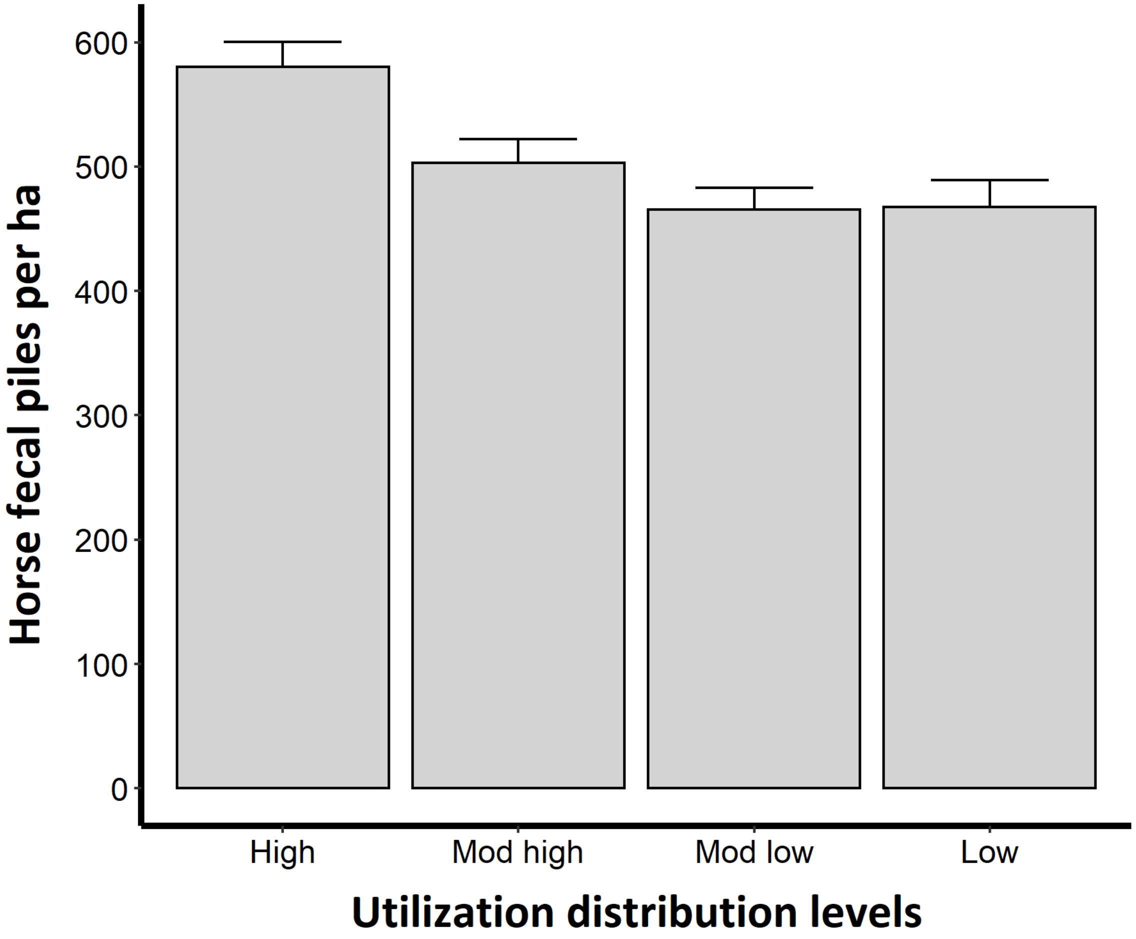

Figure 3.2. Boxplot of feral horse (*Equus ferus caballus*) fecal piles per utilization distribution level. Group means were not statistically different according to Tukey's honestly significant difference adjustments ($F_{3,127} = 1.86$, $P = 0.14$).

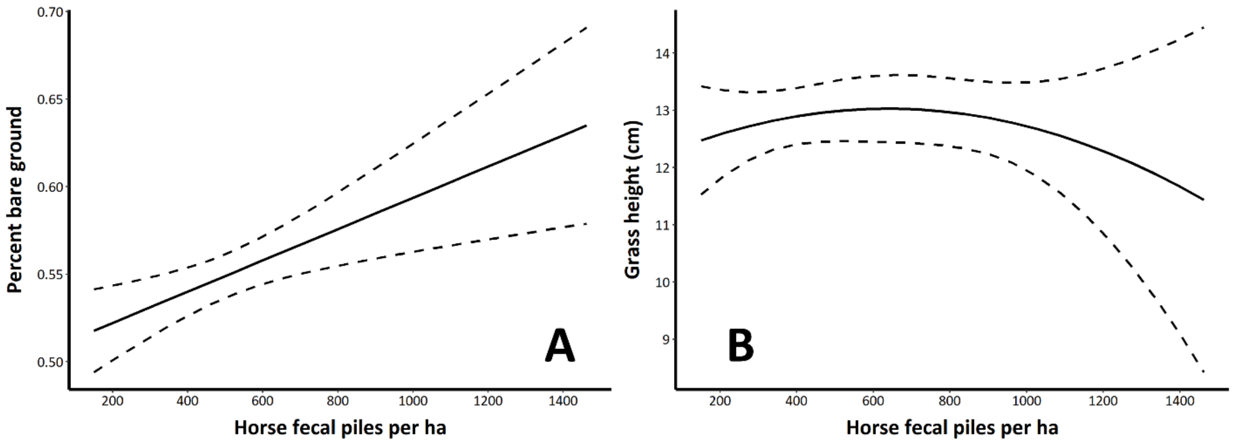

Figure 3.3. Predicted values (85% CIs) of A) percent bare ground and B) mean grass height by number of feral horse (*Equus ferus caballus*) fecal piles per hectare, Adobe Town Herd Management Area, Wyoming, USA, June through August 2018–2019. Grass height began to decline at 638 fecal piles/ha.

CHAPTER 4. Digestive morphology mediates sedentism versus nomadism in sympatric rangeland ungulates

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ABSTRACT

1. Differences in spatiotemporal resource dynamics manifest in different population-level movement syndromes, including migration, sedentism, and nomadism. Much like how migratory and sedentary behaviors occur along a spectrum, we postulate that sedentary and nomadic movements do as well. For ungulates, plant phenology dynamics, concordant with the forage maturation hypothesis (FMH), routinely drive ungulate movements, yet nearly all tests of FMH predictions involve ruminants in relatively productive areas, thus this hypothesis may have limited applicability for cecal digestors, particularly in arid systems.

2. We posited that differences in digestive morphology and feeding strategy mediate differences in resource selection and ultimately movement syndromes of sympatric ungulates. We predicted that cecal digestors should select for patches offering greater vegetation biomass rather than increased forage quality, while we predicted forage quality to be the strongest predictor of ruminant movements. In arid systems with limited forage production and water availability, digestive morphology differences suggest that cecal digestors should select for areas closer to water, while ruminants, especially concentrate selectors, should be less bound to water sources.

3. We tested this hypothesis in sympatric populations of feral horses (*Equus ferus caballus*; cecal digestors, bulk roughage feeders) and pronghorn (*Antilocapra americana*; ruminant, concentrate selector) in an arid-cold-steppe North American rangeland. We used global positioning system

(GPS) transmitters to collect location data of both ungulates, and applied a combination of semivariograms, movement metrics, and step-selection functions to quantify spatiotemporal resource dynamics, examine differences in movement syndromes, and link movement with resource dynamics.

4. Feral horses exhibited more sedentary movements largely driven by selection for predictable patches of high biomass patches and areas closer to water. Conversely, pronghorn displayed more nomadic movements, but contrary to our expectations they exhibited weak selection for patches with greater energy potential and did not select for areas closer to water.

5. Our results offer further evidence that the forage maturation hypothesis does not universally predict movements of all ungulate species and that in arid systems, water restrictions mediated by digestive strategy play an outsized role in determining resource selection and movement syndromes.

Key-words arid lands, *Antilocapra americana*, *Equus ferus caballus*, feral horse, herbivore, pronghorn, movement syndrome, nomadism, sedentism, ungulate

INTRODUCTION

Animals move to exploit variation in resources and maximize fitness. Differences in spatiotemporal resource dynamics manifest in different population-level movement syndromes, namely migration, sedentism, and nomadism (Mueller and Fagan 2008). Migratory syndromes arise in response to predictable variation between resource-rich areas that are spatially distinct (Dingle and Drake 2007). Migratory populations gain fitness advantages by performing long-distance movements while tracking the gradual change in resources between two areas (Merkle et al. 2016, Aikens et al. 2017). Conversely, animals that obtain their resource requirements in a relatively localized area exhibit sedentism (Mueller and Fagan 2008). Often populations are comprised of individuals exhibiting both syndromes with migratory and sedentary behaviors occurring along a spectrum (Cagnacci et al. 2011, Pratt et al. 2017). Nomadism has been proposed as a third movement syndrome and arises when resource variation is unpredictable across both space and time (Teitelbaum and Mueller 2019). Nomadism is understudied compared to other movement syndromes (Nandintsetseg et al. 2019), in part due to its multiple definitions and lack of clear distinction in multiple movement metrics from sedentism (Fahse et al. 1998, Roshier and Reid 2003, Fryxell et al. 2004, Abrahms et al. 2017). Both syndromes lack the repeatable directional movements between non-overlapping ranges characterized by migration; therefore, we posit that sedentary and nomadic populations inhabit a single 'range' and can also fall along a spectrum, akin to the migratory–sedentism spectrum. On the sedentary end, animals exhibit high stability in space-use throughout time with more revisits and longer time spent in the same location (Abrahms et al. 2017). Conversely, on the nomadic end, individuals show less site fidelity and move greater distances throughout the year (Abrahms et al. 2017).

In ungulate populations, spatiotemporal dynamics in vegetation production are thought to be the main driver of movement syndrome differences (Mueller et al. 2011). The forage maturation hypothesis (FMH; Fryxell 1991) is instrumental in explaining the movements of ungulates, particularly in understanding why many ungulate populations are migratory (Avgar et al. 2013, Boone et al. 2006). Measured as crude protein to fiber ratio, vegetation is of the highest quality during early growth stages, but plants attain greatest biomass late in the growing season (Fryxell 1991). Higher biomass coincides with greater proportions of fiber and subsequently lower digestibility (Fryxell 1991). For individuals to optimize energy intake, ungulates should select forage patches at an intermediate growth stage, where the curves of forage quality and quantity intersect (Fryxell 1991). In systems with available movement pathways along latitudinal or elevational gradients, ungulates can maximize exposure to optimal forage by tracking the progression of green-up between ranges (e.g., Aikens et al. 2017, Bartlam-Brooks et al. 2013). The FMH also informs understanding of resource selection and movement syndromes of ungulates across systems with varying plant phenology dynamics and constraints (e.g., Drescher et al. 2006, Hebblewhite et al. 2008, Mueller et al. 2008, Debeffe et al. 2017). Research has identified a strong conceptual link between ungulate movements and plant phenology, but nearly all tests of the FMH involve ruminants. The drivers of movement in cecal digestors have been comparatively understudied, and the applicability of the FMH in predicting patch selection of these ungulates has recently been called into question (Esmaeili et al. *Accepted*).

Irrespective of the digestive process, as fiber content increases, the rate of digestion and passage rates slow, ultimately limiting intake rate (Janis 1976, Jung and Allen 1995). However, the consequences of subsisting on a more fibrous diet manifest differently between ruminant and cecal digestors (Menard et al. 2002). Ruminant digestion is more efficient for digestion of cellulosic plant material, primarily due to the length of time material remains in the primary fermentation chamber (Janis 1976). Because the main fermentation chamber, the rumen in ruminants, is anterior to the stomach, ruminants extract more energy per unit of forage compared to cecal digestors. Consequently, as fiber content increases, the digestion process slows and the rumen is filled to capacity more often. As intake rate is directly tied to rumen fill, ruminants eat less and extract less energy from fiber-dense diets (Janis 1976). Conversely, intake rate of cecal digestors is not constrained by digestive chamber fill so these ungulates can maintain a more constant intake rate regardless of fiber content (Fleurance et al. 2010). Further complicating the influence of gut morphology on ungulate movement, cecal digestion is less efficient for water retention, relegating cecal digestors more water dependent than ruminants (Cain et al. 2012). Concordantly, cecal digestors select for areas closer to water compared to ruminants (Esmaeili et al. *Accepted*).

Digestion efficiency of cellulosic material among ungulates can be further differentiated by feeding strategy (Hofman 1989). Bulk roughage feeders subsist mainly on graminoids that have comparatively higher cellulose content than the leaves of browse (shrubs and trees) species preferred by concentrate selectors (Hofman 1989). Concentrate selectors are typically, but with notable exceptions, smaller in body size and thus have comparatively higher metabolic rates (Kleiber 1947) than larger bulk roughage feeders. It follows that small-bodied, concentrate selector ruminants should select forage patches that maximize energy potential while large-bodied, bulk rough cecal digestors should maximize forage intake.

Because patterns of resource selection should differ between sympatric ungulates with varying digestive morphologies, we predict that movement syndromes should differ as well. In non-migratory populations, we postulate that ungulates exhibit a movement syndrome along a gradient from sedentism to nomadism dependent on the spatiotemporal variation of the limiting resource respective to digestive morphology (Fig. 1). Ungulates that are most limited by forage quantity rather than quality should be relatively sedentary in systems with predictable and limited spatial variation in vegetation biomass but should become more nomadic given greater unpredictability in when and where the most productive forage patches occur. Dynamics of plant phenology should drive movement syndromes of intermediate feeding or concentrate-selecting ruminants, and they should be sedentary with consistent gradual periods of green-up (Aikens et al. 2020) and nomadic in systems with unpredictable patches of green-up, such as many arid systems (Noy-Meir 1973). Also in arid regions, dynamics water availability may be the ultimate mediator of movement syndromes (Nandintsetseg et al. 2016, 2019). Water dynamics should be most influential for cecal digestors and bulk roughage feeders but should be less important in influencing movements of concentrate selecting ruminants.

We tested the hypothesis that digestive morphology and feeding strategy mediate the expression of movement syndromes in sympatric ungulates comparing movement patterns of pronghorn (*Antilocapra americana*) and feral horses (*E. ferus caballus*). Pronghorn are concentrate-selectors that maximize crude protein and digestibility (Jakes 2015, Schwartz et al. 1977), compared to cecal digesting horses that are primarily bulk roughage feeders (Scasta et al. 2016). The contrast in digestive morphology, feeding strategy, and body size between these species offers an ideal opportunity to test our hypothesis. We predicted vegetation quantity would be less patchily-distributed and more predictable across years while timing of vegetation green-up would occur in relatively unpredictable patches between years. We also predicted that because pronghorn likely obtain a good proportion of metabolic water from vegetation they consume while horses do not, horses would show greater affinity to water. Consequently, we expected feral horses to display more sedentary movements, selecting for patches known to contain high vegetation biomass closer to water while we expected pronghorn to be more nomadic given selection for relatively unpredictable patches of vegetation green-up and less reliance on known water sources.

MATERIALS AND METHODS

Study area

We conducted our study within the Red Desert of southern Wyoming, USA. This area is classified as cold-arid-steppe (Kottek et al. 2006) with annual mean 30-year normal precipitation and temperatures of 27.7 cm and 6.0°C (PRISM Climate Group 2004) and mean elevation was 2080 m (USGS 2016). This was a shrub-dominated system with common species including Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), greasewood (*Sarcobatus vermiculatus*), yellow rabbitbrush (*Chrysothamnus viscidiflorus*), rubber rabbitbrush (*Ericameria nauseosa*), and assorted saltbush species (*Atriplex* spp.). Perennial grass species included squirreltail (*Elymus elymoides*), prairie Junegrass (*Koeleria macrantha*), inland saltgrass (*Distichlis spicata*) and sandhill muhly (*Muhlenbergia pungens*).

Animal location data

We deployed global positioning system (GPS) collars on adult female horses and pronghorn within the study area in 2017. All animal handling and use followed protocols approved by the University of Wyoming Institutional Animal Care and Use Committee (IACUC; protocol #20160826DS00249) for horses and pronghorn and Wyoming Game and Fish Department (Chapter 33-1144 Permit) for pronghorn. At no time did we have more than 30 individual horses concurrently equipped with GPS collars, adhering to criteria set forth in the DOI-BLM-WY_DO30_0104-EA Environmental Assessment. We equipped 14 horses with Lotek Wireless IridiumTrackM 3D collars (Lotek Wireless Inc., Newmarket, ON, CA) between February and March. We later equipped 23 horses with Lotek 3D collars (n = 8) and Vertex Lite GPS collars (Vectronic Aerospace GmbH, Berlin, Germany [*n* = 15]) in October. All horse collars were programmed to record locations at a two-hour period for a period of 2 years. We conducted monthly welfare checks to determine the fit of collars on each horse and detached collars if they were found in a precarious position (i.e., over the horse’s ears), or noticeable hair loss or chafing of the skin was present (Hennig et al. 2020). We captured 35 pronghorn with helicopter net-gunning (Native Range Capture Services, Ventura, California, USA) and attached store-on-board GPS/VHF collars (model G2110D; Advanced Telemetry Systems, Isanti, MN, USA) in November 2017. Transmitters were set to record locations every 4 hours over a two-year period.

Vegetation and water resources

We obtained location data from horses between 2017–2019 and from pronghorn between 2018–2019, but we calculated remotely-sensed vegetation indices from a longer time period (2010–2019) to better comprehend the spatiotemporal dynamics of vegetation production in the study system. We used MODIS MOD09A1 (250-m spatial resolution, 8-day temporal resolution) scenes to calculate the modified soil-adjusted vegetation index (SAVI; Qi et al. 1994). This metric is analogous to normalized difference in vegetation index (NDVI) but is a preferable metric for arid rangelands as it better accounts for the reflectance of bare soil (Qi et al. 1994). We followed previous methods 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 (January, February, November, December) 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 three-scene median filter (e.g., Bischof et al. 2012, Merkle et al. 2016). We calculated time-integrated SAVI (iSAVI) across the non-winter months (March – October), to quantify the amount of vegetation production per pixel per year (Pettorelli et al. 2005). To quantify forage energy potential (henceforth ‘quality’), we scaled each pixel’s yearly SAVI time-series between 0 and 1, fit a double-logistic curve to the time-series (Albeke and Merkle 2019), and calculated the first derivative of this curve to interpolate the instantaneous rate of green-up (IRG; Bischof et al. 2012, Merkle et al. 2016). IRG is a good proxy for forage quality as it reaches a maximum value where the curves of crude protein content and biomass intersect (Merkle et al. 2016).

Nearly all water locations in this arid region were anthropogenic structures including dirt tanks installed to improve feral horse distribution, stream and spring-fed reservoirs constructed for livestock and wildlife benefit, and scattered natural springs and seeps (M. Astle, BLM, personal communication). A complete record of available water sources was unavailable, so we used 2017 NAIP imagery to digitize dirt tanks and reservoirs within the study area. We added known locations of spring and seeps to the reservoir layer and then calculated the Euclidean distance to each water source.

Spatiotemporal variation

We examined spatiotemporal resource dynamics in vegetation quantity using iSAVI between March and October, and in forage quality using the date at which peak IRG occurred (Jesmer et al. 2018). We then randomly generated 10000 points within the combined minimum convex polygon of all pronghorn and horse GPS locations, then extracted dates of peak IRG and iSAVI values per point per year. We used semivariograms to quantity the amount of spatial dependency among peak IRG date and forage quantity across 500, 2500, 5000, and 10000-m spatial lags (Jesmer et al. 2018, Mueller et al. 2011). We fit variograms using the ‘gstat’ package (Gräler et al. 2016) in R version 4.0 (R Core Team 2021) and calculated the range of each fitted variogram. The range corresponds to the distance at which spatial dependency is no longer significant; therefore, larger ranges would indicate less spatial patchiness (Jesmer et al. 2018). We then used a two-sample t-test to examine whether the mean ranges per distance lag differed between peak IRG date and iSAVI at the alpha = 0.05 level. To understand relative predictability of each resource, we calculated the mean and standard deviation of each peak IRG date and iSAVI value per pixel across the 10-yr time period. We then calculated the mean coefficient of variation per metric across the study area and used a two-sample t-test to assess differences at $\alpha = 0.05$. We assumed that water locations were fixed and reservoir volume followed a predictable time-series of highest in early spring (March/April) and lowest in summer (July/August). Therefore, we assumed that distance to water was highly predictable across space and time.

Movement metrics

We first rarified the horse location dataset (2-hr fix rate) to match the pronghorn fix rate (4-hr). For each horse and pronghorn, we then calculated a suite of movement metrics shown to help differentiate between sedentary and nomadic movement syndromes (Abrahms et al. 2017, Bracis et al. 2018, Nandintsetseg et al. 2019). These metrics included maximum net squared displacement, number of revisits per location, total residency time per location, and percent overlap of monthly 95% utilization distributions (Abrahms et al. 2017, Nandintsetseg et al. 2019; Table 1). Net squared displacement is expected to be greater for nomads, while the number of revisits, total residency time, and percent overlap in monthly utilization distributions should be greater for sedentary individuals (Abrahms et al. 2017, Bracis et al. 2018. Nandintsetseg et al. 2019). We calculated monthly utilization distributions using dynamic Brownian Bridge movement models (Kranstauber et al. 2012) within the ‘move’ package (Kranstauber et al. 2019) and used the Bhattacharyya’s affinity (Bhattacharyya 1943) to quantify overlap (Fieberg and Kochanny 2005; Clapp and Beck 2015). We calculated maximum net squared displacement using the ‘adehabitatLT’ package (Calenge 2006), and number of revisits and residency time using the ‘recurse’ package (Bracis 2018). We used a 435-m radius for pronghorn and a 560-m radius for horses per location to calculate the number of revisits and residency time as these were the median step lengths for each respective population. We set a threshold of 8 hours for both species to eliminate brief excursions outside of the radius (Nandintsetseg et al. 2019). We used a two-sample t-test to examine whether the metrics differed between populations.

Selection of resources

Even if the movement syndromes per population and spatiotemporal resource dynamics matched our predictions, it is also important to demonstrate that each species indeed selected for the predicted resource(s) based on gut morphology as they moved across the landscape. Therefore, we modeled step-selection functions (Thurfjell et al. 2014) using the 'glmmTMB' package (Brooks et al. 2017) to examine relative strength of selection for forage quantity, forage quality, and distance to water. We limited our analyses to between 21 March and 30 June to coincide with the growing season. We generated 10 available steps per each used step by sampling from an observed distribution of each individual's step lengths and turn angles (Latham et al. 2011). We randomly selected one step per individual per day to reduce the influence of spatiotemporal autocorrelation.

To assess relative strength of selection among variables, we centered and scaled all variables to a mean of zero and a standard deviation of one (Schielzeth 2010). We first built a base model by evaluating univariate models of variables predicted to also influence selection (Table 2). We incorporated the log of distance between locations in each model along with a random intercept and slopes for each individual by year combination (Muff et al. 2020). We calculated 85% confidence intervals for each variable (Arnold 2010) and brought forth all variables with confidence intervals not overlapping 0 into a base model. For highly correlated variables (r >0.6), we ranked each model using Akaike's Information Criterion (AIC; Burnham and Anderson 2002) and brought forth the top-ranked variable. Next we evaluated a candidate model set that included all additive combinations of iSAVI, IRG, and distance to water (8 models total). The base variables were included as fixed effects in all models. We ranked the candidate models by AIC and model averaged within models <4 AIC to obtain coefficient values and 85% confidence intervals (Arnold 2010).

RESULTS

We collected 62,857 locations from 27 pronghorn that were collared for a mean duration of 19.0 months (SD = 5.8 months). We recorded 15 mortalities of collared individuals, though we classified only 1 mortality as captured-related (i.e., occurring within 3 weeks of capture date; Reinking et al. 2018). We obtained 59,079 locations from 26 feral horses that were collared for 17.9 months (SD = 7.6 months) and recorded no mortalities.

Mean semivariogram ranges for date of maximum forage quality and overall vegetation quantity were significantly different across 500, 2500, and 5000-m lags ($P < 0.001$), but not different at 10000-m lags (Fig. 2). The mean coefficient of peak IRG date across the 10-year period was 0.16 ($\bar{x}$ = 110.8, SD = 17.3) compared to 0.09 ($\bar{x}$ = 3.0, SD = 0.26) for forage quantity, and these means were statistically different ($P < 0.001$), demonstrating that peak forage quality was more patchily distributed and unpredictable across years compared to total above ground vegetation biomass. Across all movement metrics, pronghorn exhibited more nomadic movements compared to the more sedentary movements of feral horses (Fig. 3). Pronghorn had significantly lower mean proportion of overlap among monthly home ranges (0.21 vs. 0.39), greater maximum net squared displacement (1088.6 km vs. 268.9 km), fewer revisits (14.6 vs. 52.4), and shorter residency times (134.0 vs. 486.5) than horses, respectively.

Regarding step-selection functions, both distance to water and vegetation quantity received 100% of the model weight for feral horses, while forage quality received no model support (Table 3). Feral horses exhibited the strongest selection for patches with higher vegetation quantity (β = 1.03, 95% CIs = 0.66, 1.40), followed by less topographically rough areas (β = -0.40, CIs = -0.46, -0.35), greater proportion of herbaceous cover (β = 0.216, CIs = 0.17, 0.26), and areas closer to water (β = -0.113, CIs = -0.21, -0.01; Table 4). Vegetation quantity also received 100% of the model weight for pronghorn, whereas distance to water received 42% and forage quality received 20% (Table 5). Like horses, pronghorn exhibited the strongest selection for vegetation quantity (β = 1.310, CIs = 0.85, 1.77), followed by less topographically rough areas (β = -0.325, CIs = -0.38, -0.27). Model-averaged coefficients indicated weak selection for forage quality (β = 0.01, CIs = -0.01, 0.13) and areas farther from water (β = 0.03, CIs = -0.01, 0.13), but confidence intervals for both variables overlapped 0 (Table 6).

DISCUSSION

We tested the hypothesis that digestive morphology mediates the movement syndromes of sympatric ungulates. We compared movement metrics and resource selection of feral horses (bulk roughage selecting cecal digestors) and pronghorn (concentrate selecting ruminants) in an arid cold desert system where both water and forage can be limiting. Our predictions of vegetation dynamics held true as values of vegetation biomass per 250-m pixel were more similar to each other at most spatial lags, and more predictable across years than the timing of green-up. As expected, feral horses exhibited more sedentary movements driven by selection for high biomass patches close to water. Conversely, pronghorn were not tied to water sources and displayed more nomadic movements though they exhibited only weak selection for patches offering the greatest energy potential, a result contrary to our expectations.

Our results offer further evidence that the FMH does not universally predict movements of all ungulate species (Esmaeili et al. *In review*). In arid regions with meager herbaceous vegetation production, there is likely little nutritional advantage for horses to track small differences in vegetation quality. Their relatively inefficient digestive system likely renders any increase in quality insignificant, especially if that means moving into areas where water is less predictable. Hence, because vegetation production was similar across space and predictable among years, feral horse movements were relatively sedentary characterized by stable home ranges near known water locations.

In arid regions, cecal digestors likely receive only a small proportion of their water needs from forage and are thus highly dependent on available water sources (Kaczensky et al. 2010, Nandintsetseg et al. 2017). Our results indicate horses were more tied to known water locations than pronghorn; thus, predominantly man-made water catchments may play an outsized role in the movement syndrome of this feral horse population. Because feral horse grazing can have negative effects on ecosystems (Eldridge et al. 2020), water developments were installed to more evenly distribute horse use across the landscape. A side-effect of adding these water sources is that they promote repeated use of the same areas, thereby affording little or no rest for plant species that did not co-evolve with high grazing pressure (Mack and Thompson 1982). A central tenet of livestock management is properly manipulating the timing, intensity, and frequency of grazing to maintain desired rangeland function (Holechek et al. 2004). Indeed, intensity of horse use in this system was linked to greater proportions of bare ground (Hennig et al. *In review*). We think that if anthropogenic reservoirs were unavailable in this system, horses may switch to a more nomadic syndrome moving between sparsely located natural water sources, similar to the water-driven nomadism of equids in the Gobi Desert (Nandintsetseg et al. 2016, 2019).

Further contradicting the FMH, our metric of vegetation quality (IRG) received little model support for explaining pronghorn selection during the growing season. This presented us with a less clear-cut explanation for why movement metrics differed between horses and pronghorn. We believe the observed differences can be explained by 2 factors. First, even minor tracking of relatively unpredictable green-up could result in more nomadic movements than horses. Second, pronghorn movements were independent of known water sources during the growing season. Plants are most succulent during this season, and pronghorn use of free-standing water typically is inversely correlated with succulence and quantity of preferred forage (Beale and Smith 1970). Further, pronghorn possess higher body water content than other ruminants indicating low reliance on water (Wesley et al. 1970). Though we have documented pronghorn use of anthropogenic water sources in this area (Hennig et al. 2021), our results indicate such use may be more opportunistic in nature. Consequently, pronghorn have the ability to wander farther from water in exploration of forage patches translating into more nomadic movements.

The relatively weak selection by pronghorn for higher forage quality patches was still surprising. We expected pronghorn movements to maximize energy potential given their smaller body size and concentrate feeder strategy, especially given that at least some individuals of several pronghorn populations maximize energy potential by undergoing migration in myriad systems of the western United States (e.g. Jakes et al. 2018, Kolar et al. 2011, Sawyer et al. 2005). So why do none of the pronghorn inhabiting this system migrate? Moving south and east out of this arid system offers an elevational gradient providing more vegetation production than that which is available within the Red Desert. Indeed, mule deer (*Odocoileus hemionus*), another ruminant concentrate feeder, winter within portions of our study site, but many migrate to the aforementioned more productive areas during the spring and summer (Kauffman et al. 2020). The answer to why pronghorn do not migrate may simply be that they are able to meet their energetic needs within the system; however, they also face barriers to movement that may prevent migration and associated potential increases in energy acquisition. While mule deer can cross both fences and roads on migration paths (Sawyer et al. 2013), these anthropogenic features have proven to be much more restrictive for pronghorn (Reinking et al. 2019; Xu et al. 2020). Much of the interior of our study site was unfenced and lacked major roads, but fences, highways, and a railroad paralleled the boundaries of our system, and we observed multiple GPS-collared pronghorn approaching major highways but never crossing.

Our research provides further insight into the role that ungulate digestive systems play in resource selection and movement syndromes. We found that the FMH may have limited applicability to cecal digestors and even ruminants inhabiting arid systems. Vegetation quality appears to be less significant in explaining differences in movements between dryland ungulates than water availability. Water-driven nomadism has been documented by both cecal digestors and ruminants in the Gobi Desert, but there appears to be a threshold where forage dynamics becomes a more important driver of ungulate movements (Nandintsetseg et al. 2019). Identifying species- and system-specific thresholds of water limitation can help inform conservation and management actions for both wild and domestic ungulates, especially in the face of global climate change.

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Tables and figures

Table 4.1. Description of calculated movement metrics and predicted responses of each metric to sedentism versus nomadism.

Metric	Description	Sedentism	Nomadism
Number of revisits	Times that an individual returned to the same location	Higher	Lower
Residency time	The sum of hours spent at a location	Higher	Lower
Bhattacharyya's affinity	Percent overlap in volume between monthly 95% utilization distributions	Higher	Lower
Maximum net squared displacement	Maximum displacement between any two locations	Lower	Higher

Table 4.2. Sources of variables used in step-selection functions for feral horses and pronghorn, Red Desert, Wyoming, USA, March–June, 2017–2019.

Variable	**Source**
Proportion bare ground	NLCD 2016 All Rangeland Fractional Components [a]
Proportion herbaceous cover	NLCD 2016 All Rangeland Fractional Components [a]
Proportion sagebrush cover	NLCD 2016 All Rangeland Fractional Components [a]
Proportion all shrub cover	NLCD 2016 All Rangeland Fractional Components [a]
Distance to well pad	Active oil and gas wells [COGCC (2020) [b] & WOGCC (2020) [c]]
Topographic ruggedness index	Digital elevation model (USGS 2016) [d]
Compound topographic index	Digital elevation model (USGS 2016) [d]
Heat load index	Digital elevation model (USGS 2016) [d]
Slope position	Digital elevation model (USGS 2016) [d]
Distance to water	NAIP 2017 aerial imagery [e]
Time-integrated soil-adjusted vegetation index (iSAVI)	MODIS MOD09A1 [f]
Instantaneous rate of green-up (IRG)	MODIS MOD09A1 [f]

[a] Rigge et al. (2020): https://www.mrlc.gov/data?f%5B0%5D=category%3ARangeland%20%E2%80%93%20Basemap

[b] COGCC (2019): https://cogccmap.state.co.us/cogcc_gis_online/

[c] WOGCC (2019): retrieved from Wyoming Geographic Information Science Center https://services.wygisc.org/HostGIS/rest/services/GeoHub/WOGCCActiveWells/MapServer/0

[d] Calculated using ArcGIS Geomorphometry & Gradient Metrics Toolbox (Evans et al. 2014)

[e] Retrieved from Wyoming Geographic Information Science Center https://data.geospatialhub.org/app/108afdf1d38e4377a4444cab725b5624

[f] https://lpdaac.usgs.gov/products/mod09a1v006/

Table 4.3. Model selection results for feral horse step-selection functions, Red Desert, Wyoming, USA, March–June, 2017–2019.

Model	**K**	**AIC**	**ΔAIC**	w_i
Distance to water + iSAVI [a]	13	104799.2	0.00	0.85
Distance to water + iSAVI + IRG [b]	15	104802.7	3.47	0.15
Distance to water	11	104825.2	26.01	0.00
Distance to water + IRG	13	104828.2	29.05	0.00
iSAVI	11	104835.7	36.52	0.00
iSAVI + IRG	13	104839.2	40.01	0.00
Base	9	104863.9	64.72	0.00
IRG	11	104866.9	67.73	0.00

[a] Time-integrated soil adjusted vegetation index

[b] Instantaneous rate of green-up

Table 4.4. Model-averaged coefficients indicating relative strength of selection by feral horses, Red Desert, Wyoming, USA, March–June, 2017–2019.

Model	**Estimate**	**85% CIs**
Log(dist)	-0.072	-0.095, -0.050
% herbaceous cover	0.216	0.174, 0.260
TRI [a]	-0.401	-0.455, -0.347
HLI [b]	0.025	-0.007, 0.057
Distance to water	-0.113	-0.213, -0.014
iSAVI [c]	1.029	0.657, 1.402
IRG [d]	-0.002	-0.057, 0.034

[a] Topographic ruggedness index
[b] Heat load index
[c] Time-integrated soil adjusted vegetation index
[d] Instantaneous rate of green-up

Table 4.5. Model selection results for pronghorn step-selection functions, Red Desert, Wyoming, USA, March–June, 2017–2019.

Model	**K**	**AIC**	**ΔAIC**	w_i
iSAVI [a]	7	109385.8	0.00	0.46
Distance to water + iSAVI	9	109386.4	0.61	0.34
iSAVI + IRG [b]	9	109388.5	2.70	0.12
Distance to water + iSAVI + IRG	11	109389.2	3.38	0.08
Base	5	109425.5	39.73	0.00
Distance to water	7	109426.0	40.16	0.00
IRG	7	109428.9	43.05	0.00
Distance to water + IRG	9	109429.3	43.52	0.00

[a] Time-integrated soil adjusted vegetation index

[b] Instantaneous rate of green-up

Table 4.6. Model-averaged coefficients indicating relative strength of selection by pronghorn, Red Desert, Wyoming, USA, March–June, 2017–2019.

Model	**Estimate**	**85% CIs**
Log(distance)	0.011	-0.005, 0.029
% shrub cover	-0.217	-0.226, -0.178
TRI [a]	-0.325	-0.379, -0.271
Distance to water	0.025	-0.010, 0.130
iSAVI [b]	1.310	0.851, 1.770
IRG [c]	0.006	-0.008, 0.130

[a] Topographic ruggedness index
[b] Time-integrated soil adjusted vegetation index
[c] Instantaneous rate of green-up

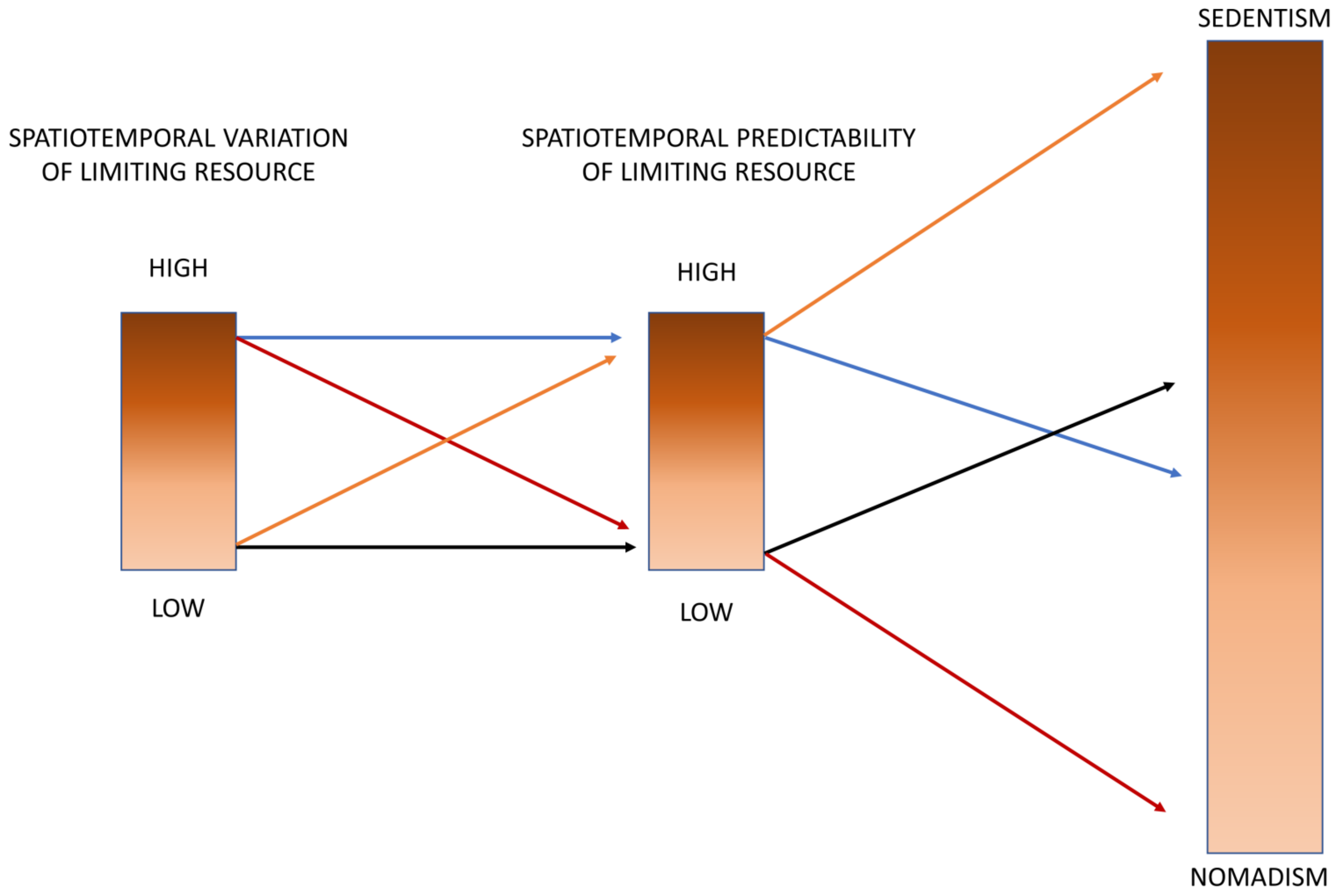

Figure 4.1. Hypothetical relationship between resource variation and predictability in determining where along the gradient of sedentism to nomadism a population falls. For example, the orange arrow represents a population inhabiting an environment with low spatiotemporal variation and high predictability of its limiting resource, therefore the population is expected to be highly sedentary.

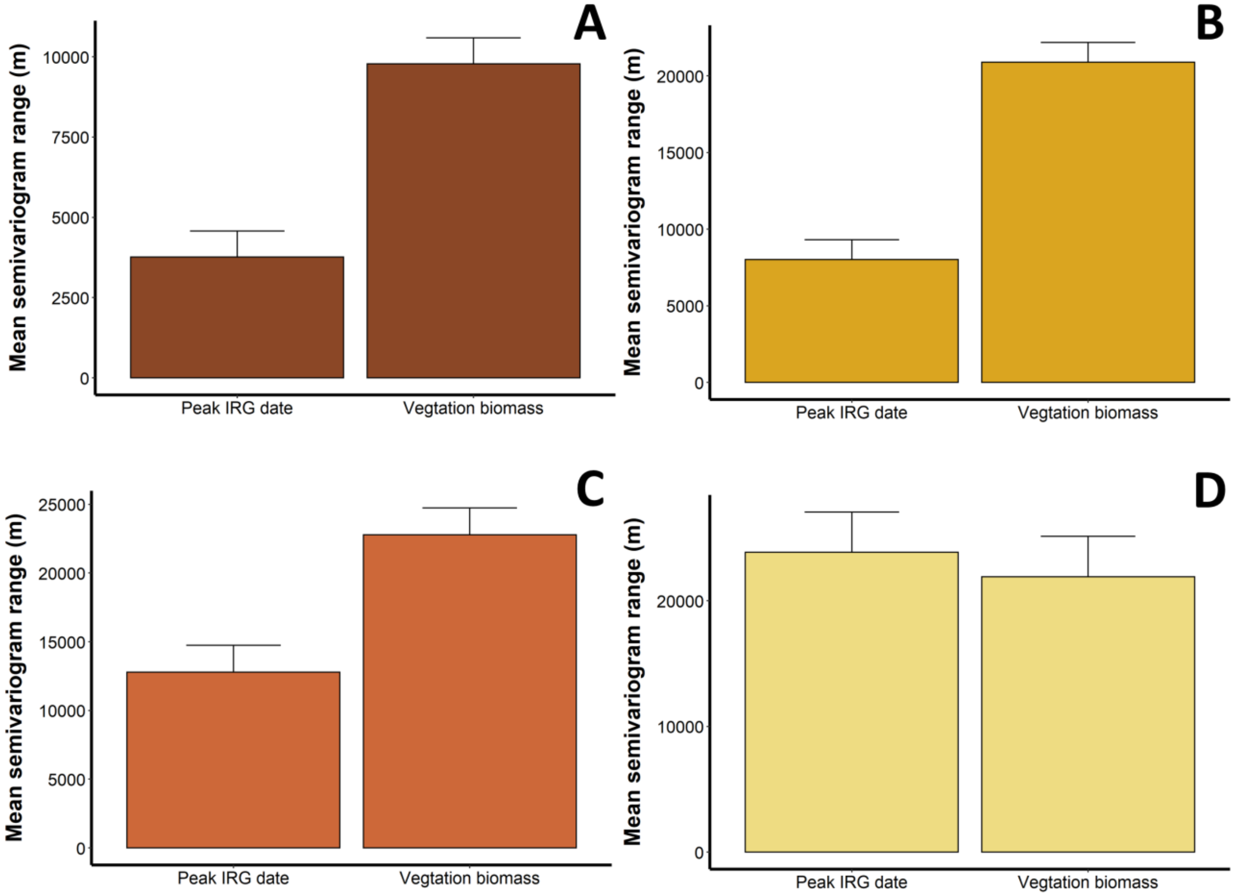

Figure 4.2. Mean semivariogram ranges of vegetation production (calculated using time-integrated soil-adjusted vegetation index) and date of peak instantaneous rate of green-up (IRG) calculated across (A) 500-m, (B) 2500-m, (C) 5000-m, and (D) 10000-m spatial lags, Red Desert, Wyoming, USA, 2010–2019.

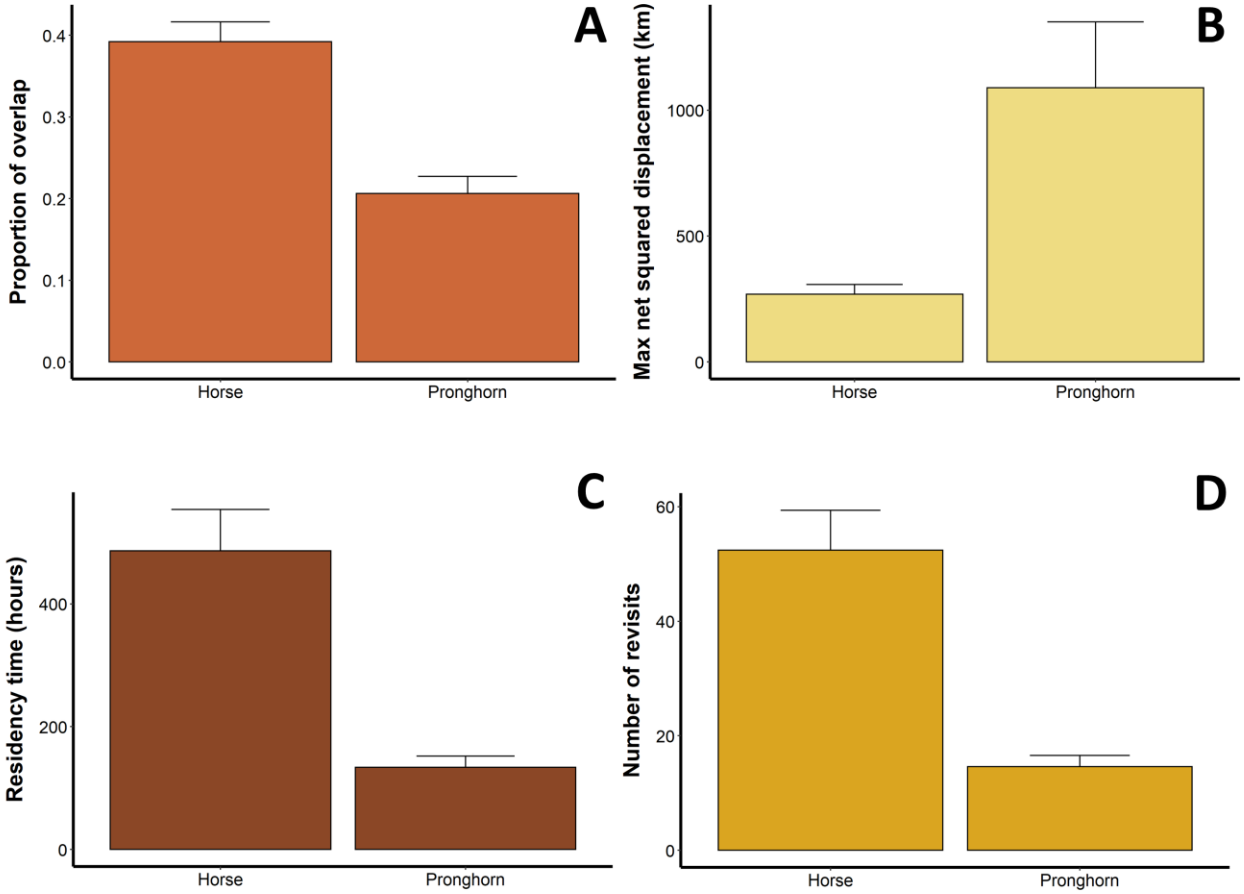

Figure 4.3. Population means and standard errors of (A) proportion of overlap (using Bhattacharyya's affinity) of monthly 95% utilization distributions, (B) maximum net squared displacement, (C) total residency time per location (hours), (D) number of revisits per location, calculated for pronghorn and feral horses, Red Desert, Wyoming, USA, 2017–2019.

CHAPTER 5. Resource selection and occurrence overlap between feral horses, greater sage-grouse, and pronghorn in cold-arid-steppe

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ABSTRACT

Feral horse (*Equus ferus caballus*) populations on public rangelands in the western United States continue to increase, potentially impacting co-occurring wildlife species. Feral horses may negatively affect two iconic western species, greater sage-grouse (*Centrocercus urophasianus*; hereafter ‘sage-grouse’) and pronghorn (*Antilocapra americana*) through mechanisms of habitat alteration and competition. Wyoming contains the largest global populations of both pronghorn and sage-grouse and the ranges of these species overlap with feral horses most in Wyoming compared to other states. Therefore, evaluation of potential horse impacts to pronghorn and sage-grouse within the state have implications at local, state, and global levels. While their ranges overlap, we lack understanding of comparative resource selection and space use among horses, pronghorn and sage-grouse within specific horse management areas, but this information is critical to implement successful management strategies. To address this knowledge gap, we captured and attached global positioning system (GPS) transmitters to female horses (n = 30), pronghorn (n = 30), and greater sage-grouse (n = 46) within the Bureau of Land Management–Adobe Town Herd Management Area in southern Wyoming between 2017 and 2021 to evaluate seasonal resource selection and predicted proportion of overlap in occurrence among species. Resource selection was most similar between pronghorn and horses, with a high degree of predicted occurrence overlap in both summer (0.84) and winter seasons (0.90). Horse and sage-grouse overlap was lowest during the sage-grouse breeding (0.68) and winter (0.62) seasons, but selection by both species for closer proximity to water and herbaceous cover resulted in a high degree of occurrence overlap (0.91) in the summer. Our results suggest that pronghorn face potential competition with horses year-round in this area, whereas the threat of decreased habitat quality is most prevalent for sage-grouse during later brood-rearing. Our work can help guide placement of potential management actions, whereas future research should examine links between feral horse effects and fitness metrics of pronghorn and sage-grouse.

KEY WORDS *Antilocapra americana*, breeding, *Centrocercus urophasianus*, *Equus ferus caballus*, habitat selection, water use, winter, Wyoming

INTRODUCTION

Management of controversial feral animals is an increasingly common issue in the Anthropocene (Boyce et al. 2021). In the western U.S., feral horse (*Equus ferus caballus*) abundance continues to increase on public lands, threatening the provisioning of ecosystem services (Scasta et al. 2018). Potential competition with livestock has long been a concern regarding feral horses given their strong diet overlap and potential to decrease rangeland quality (Scasta et al. 2016; Beever et al. 2008). Feral horse grazing can decrease vegetation biomass, increase soil compaction, 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. *In review*). Comparatively, the indirect and direct effects that this feral species has on native fauna is less understood; but critical assessment is imperative (Danvir et al. 2018). 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). The frequency and degree of horse-related effects is projected to increase (Eberhardt et al. 1982, Garrott and Oli 2013), therefore a pressing need exists to better understand area-specific potential for feral horses to affect wildlife species, especially species of concern.

Controlling population sizes or manipulating the distribution of feral horses to mitigate their detrimental effects is complicated owing to their protected status under the Wild Free-roaming Horses and Burros Act of 1971 (Public Law 92-195). This federal legislation designates horses and burros as natural components of western ecosystems due to their cultural significance to many U.S. citizens (Public Law 92-195). Equid abundances are to be balanced with the ecological integrity of western rangelands, but management actions are restricted to maintain a free-roaming status for equids (Public Law 92-195). Importantly, the Act pertains only to equids inhabiting federal land where they existed at the time of its passage (Public Law 95-514). These management boundaries are known as Herd Management Areas (HMA) on Bureau of Land Management (BLM) jurisdiction and Wild Horse and Burro Territories on U.S. Forest Service (USFS) land.

Many management areas overlap with the ranges of greater sage-grouse (*Centrocercus urophasianus*; henceforth 'sage-grouse') and pronghorn (*Antilocapra americana;* Beever and Aldridge 2011, Stoner et al. 2021); two iconic species that have undergone recent population declines, particularly sage-grouse (Connelly and Braun 1997, Yoakum and O'Gara 2000). The state of Wyoming contains >50% of the global pronghorn population and approximately 40% of the sage-grouse population (Yoakum and O'Gara 2000, Doherty et al. 2010c), making management efforts for these species within Wyoming a major priority at both the state, continental, and global levels. Wyoming also contains the second highest abundance of feral horses, and of all the western states, the degree of range overlap between feral horses with pronghorn and sage-grouse is greatest within Wyoming (BLM 2021; Beever and Aldridge 2011; Stoner et al. 2021). Considering the high degree of range overlap, both species may be susceptible to habitat degradation and/or competition from horses, but data concerning these interactions is limited (Stoner et al. 2021).

There is sparse, but emergent information concerning the influence feral horses have on sage-grouse while multiple sources have listed horses as a potential threat to sage-grouse populations (Southwest and South Central Wyoming Local Sage-grouse Working Groups, unpublished reports; Beever and Aldridge 2011, USFWS 2013). Indirect impacts mainly stem from habitat alteration consisting of decreased native grass and shrub cover, lower vegetation height and densities, increases in exotic grass cover and bare ground, and greater prevalence of unpalatable forbs (Beever and Aldridge 2011, Davies et al. 2014, Boyd et al. 2017, Hennig et al. *in review*). Direct impacts are also a concern, however, as researchers have demonstrated that horse presence can disturb sage-grouse during lekking, a critical time-period for this species (Muñoz et al. 2020). Pronghorn are thought to be more affected from competition with feral horses. In water-limited regions, the presence of feral horses can lead to temporal overlap at watering points (Hennig et al. 2021), resulting in altered watering activity patterns and increased time spent vigilant at water sources (Hall et al. 2018; Gooch et al. 2017). Though the feeding strategies of horses (bulk-grazer and cecal digester; Janis 1976) and pronghorn (concentrate feeder and rumen digester; Jakes 2015) differ, forage competition is also a concern at sites with limited herbaceous production, especially during harsh winters (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, quantification of resource selection and occurrence overlap within feral horse management areas is absent. Such information could assist managers with identifying seasonally important resources for each species and elucidating areas where potential habitat alteration and competition stemming from horse activity may be greatest. To address this pressing need, we examined resource selection of co-occurring feral horse, pronghorn, and sage-grouse populations within the Adobe Town HMA in southern Wyoming, USA. Our objectives were to: 1) compare seasonal resource selection between horses and sage-grouse, and horses and pronghorn, 2) quantify the amount of predicted overlap between these species comparisons, and 3) create spatially explicit maps depicting relative degree of occurrence overlap between horses and each species on a seasonal basis.

STUDY AREA

We conducted our study within the 3,413 km^2 Adobe Town HMA in southcentral Wyoming, USA (Fig. 1). Elevation ranged from 1883–2506 m (USGS 2016) and annual 30-year normal mean precipitation and temperature were 27.7 cm and 6.0°C, respectively (PRISM Climate Group 2004). The area was a shrubland-dominated ecosystem with common species including Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), rubber rabbitbrush (*Ericameria nauseosa*), yellow rabbitbrush (*Chrysothamnus viscidiflorus*), greasewood (*Sarcobatus vermiculatus*), spiny hopsage (*Grayia spinosa*), shadscale (*Atriplex confertifoli*a) and Gardner’s saltbush (*A. gardneri*). Grass production was low compared to much of the surrounding Wyoming Basin, but common species included prairie Junegrass (*Koeleria macrantha*), bottlebrush squirreltail (*Elymus elymoides*), Sandberg bluegrass (*Poa secunda*), and sandhill muhly (*Muhlenbergia pungens*). The region also contained the Powder Core Area for greater sage-grouse (Doherty et al. 2011, State of Wyoming 2011) and two areas classified by the

Wyoming Game and Fish Department (WGFD) as crucial yearlong ranges for pronghorn (WGFD 2021; Fig.1). Other land-uses included livestock ranching and fossil fuel exploration and extraction.

METHODS

Animal relocation data

We deployed iridium-based global positioning system (GPS) collars (Lotek Wireless IridiumTrackM 3D collars [Lotek Wireless Inc., Newmarket, Ontario, Canada & 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 store-on-board GPS collars (model G2110D; Advanced Telemetry Systems, Isanti, Minnesota, USA) on adult female pronghorn in November 2017. 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 pronghorn (Native Range Capture Services, Ventura, California, USA) and fit collars at the capture location. We programmed GPS transmitters to record locations every 2 hours for horses and every 4 hours for pronghorn and set all collars to remotely detach after a period of 2 years.

Beginning in April 2018, we deployed rump-mounted GPS transmitters (22-g GPS PTT [GeoTrack, King George, Virginia, USA and 15-g Bird Solar [e-obs GmbH, Grunwald, Germany]) on female sage-grouse captured across our study area and the adjacent Atlantic Rim (Kirol et al. 2015) through spot-lighting and hoop-netting (e.g., see Smith et al. 2016). We continued to capture and attach transmitters to sage-grouse each December and April 2018–

2020. To meet the objectives of a concurrent study, we programmed transmitters to collect between 4 and 17 locations per day depending on the season.

All feral horse handling and use followed protocols approved by the University of Wyoming Institutional Animal Care and Use Committee (IACUC; protocol #20160826DS00249) and at no time were more than 30 individual horses concurrently equipped with GPS collars, adhering to criteria set forth in the DOI-BLM-WY_DO30_0104-EA Environmental Assessment. Pronghorn and sage-grouse were captured, handled, and monitored in accordance with respective protocols approved by the Wyoming Game and Fish Department (Chapter 33-1144 and Chapter 33-1160 Permits) and University of Wyoming IACUC (protocols 20160826DS00249 and 20170324AP00266).

Season classification

Sage-grouse habitat selection differs seasonally (Fedy et al. 2014), with distinct habitat preferences during the breeding, summer, and winter seasons (Pratt et al. 2019). Therefore, we delineated the yearly calendar into 3 seasonal periods for sage-grouse: winter (November – March), breeding (April – June), and summer (July – October). We set dates for each season by first fitting double-logistic curves of net-squared displacement by date to identify migratory individuals (Bunnefeld et al. 2011, Singh et al. 2012). 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 2020) 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 date ranges closely matched statewide (Wyoming) averages of winter, breeding, and summer seasons for sage-grouse (J. L. Beck, unpublished data). We separated pronghorn habitat use into summer and winter following Reinking et al. (2019). We used the same winter date range as we did for sage-grouse to elicit comparisons across all 3 species. We classified the remaining months (April – August) as summer but removed September and October locations as pronghorn were exposed to hunting during these months which likely influences movements. We did not identify unique seasons for feral horses; instead we evaluated selection of horses relative to each of the aforementioned seasons.

Predictor variables

We compiled a list of variables thought to be biologically relevant for understanding resource selection of each species per season (Table 1). We used the National Land Use Consortium Dataset - All Rangeland Fractional Components (NLCD 2016) to assess the proportion of each 30-m pixel classified as bare ground, herbaceous cover, sagebrush cover, and total shrub cover. We calculated topographic variables (topographic ruggedness index [TRI], compound topographic index [CTI], heat load index [HLI], slope position) from a 30-m digital elevation model (USGS 2016) using the ArcGIS Geomorphometry & Gradient Toolbox (Evans et al. 2014) within ArcMap 10.6 (ESRI 2020). We calculated straight-line distances to water for each 30-m pixel from a digitized layer of water reservoirs and known locations of springs and seeps (Chapter 4). We also calculated straight-line distance to active oil and gas well pads using datasets retrieved from the Wyoming and Colorado Oil & Gas Conservation Commissions (WOGCC 2020, COCGG 2020). We used MODIS 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 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 (January, February, November, December) 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 three-scene median filter (e.g., Bischof et al. 2012, Merkle et al. 2016). We calculated the time-integrated version of this index (iSAVI) to represent overall vegetation biomass produced during the breeding and summer seasons per year (Pettorelli et al. 2005). We resampled all variables to a 30-m spatial resolution and calculated a moving window average (500-m radius) to evaluate selection at a broader scale. We initially considered inclusion of moving-window averages at 1500, 3200, and 6400-m radii (Fedy et al. 2014), but preliminary analyses revealed poor predictive power using these broader scales. We attributed this to non-stationarity in our study area as proportion of herbaceous cover, sagebrush cover, total shrub cover, and iSAVI all increase going from the core to the edges of our study area. In other words, models including variables at these scales resulted in occurrence predictions superficially similar to a density of collected locations, with little or no occurrence in areas in novel areas. In evaluating winter resource selection, we chose to include distance to water as a covariate even though most free-standing water was frozen during this time period. We knew that horses exhibited relatively stable home ranges driven in part by distances to water (Chapter 4); therefore, we postulated that distance to water was a reasonable year-round predictor. We also included iSAVI produced during the preceding summer with the assumption that greater growing season production would translate into greater amounts of residual forage during the winter.

Generating availability

Our sage-grouse telemetry dataset included individuals that never or only partially overlapped spatially with our GPS-collared horses and pronghorn; therefore, we removed all locations that fell east of Wyoming State Highway 789, south of the Little Snake River, and south of Moffat County, Colorado Road 4 to better match the spatial distribution of horses and pronghorn. To limit influence of individuals with few locations in resource selection models, we chose to retain pronghorn and horses with >500 locations per season. Due to fewer grouse locations, we kept individuals with >200 locations per season. We generated minimum convex polygons (MCP) around the retained locations of each population per season and generated 10 random points per used location within this population-wide polygon. We then extracted predictor variables at each used and random (background or available) location (Table 1).

Fitting models

We fit all models using the ‘glmmTMB’ package (Brooks et al. 2017) following the framework presented in Muff et al. (2020). We fit infinitely weighted logistic regression models (Wharton and Shepard 2010, Fithian and Hastie 2013) between used and background locations with random intercepts and slopes for each individual by year combination (Gillies et al. 2006, Muff et al. 2020). Logistic regression approximates an inhomogeneous Poisson process (IPP) when the number of background points is sufficiently large (Wharton and Shepard 2010). This results in consistent and unbiased parameter estimates and facilitates interpretation as the number of expected presences per unit area (Wharton and Shepard 2010, Fithian and Hastie 2013). Incorporating a large number of background points is computationally inefficient, so we set each background point to a value of 1000 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). We first compared univariate models of all variables and scales (30 and 500-m) to a null, intercept-only, model using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). The top-ranked scale per variable was brought forward for consideration in a global model if it performed better than the null. We also used AIC to assess which among highly correlated variables ($|r| > 0.6$) should be retained. We then fit a global model and extracted coefficients and 95% confidence intervals for all variables.

Occurrence overlap

We generated spatially-explicit rasters of predictive occurrence based on a global model for each species per season. We did this by re-running models using the un-scaled variables and extracting fixed-effect coefficients to estimate an RSF of the following form:

$$w(\mathrm{x}) = \exp[\beta_1 \mathrm{h}_1(\mathrm{x}) + \beta_2 \mathrm{h}_2(\mathrm{x}) + \ldots + \beta_n \mathrm{h}_n(\mathrm{x})]$$

where $w(\mathrm{x})$ is the proportional probability of selection, β_n are fixed-effect coefficients, and h_n is the value of a variable at location x. We mapped models results to a 30-m raster of our study area and then clipped the raster to a polygon representing all livestock grazing allotments within the Adobe Town HMA. In other words, we evaluated predicted occurrence overlap in areas where management actions were most likely to occur. We divided each 30-m pixel value by the sum value of the predicted raster, resulting in a raster summing to 1. We then calculated Bhattacharyya's affinity (Bhattacharyya 1943) between predicted rasters to quantify the proportion of overlap in occurrence between species per seasons (Fieberg and Kochanny 2005, Clapp and Beck 2015, Pratt et al. 2019). We then generated spatially explicit maps of relative occurrence overlap by dividing each raster into 5 equal quantiles and considered Bhattacharyya's affinity values of >0.6 to represent moderately high overlap and >0.8 to indicate high overlap.

RESULTS

We used location data from 30 female feral horses, 30 female pronghorn, and 46 female sage-grouse to evaluate resource selection for each species across biologically relevant seasons between 2017–2019 for horses and pronghorn, and between 2018–2021 for sage-grouse. Stratified by season and species, we used 21,599 horse locations from 48 unique animal by year combinations (AY), and 11,547 sage-grouse locations (30 AY) during the sage-grouse breeding season; 23,553 horse locations (43 AY) and 9,391 sage-grouse locations (24 AY) during the sage-grouse summer season; 41,795 horse (47 AY) and 39,953 (44 AY) pronghorn locations during the pronghorn summer season; and 35,940 (40 AY), 42,590 (50 AY), and 14,190 (36 AY) locations of horses, pronghorn, and sage-grouse during the sage-grouse winter season. We documented 23 sage-grouse and 15 pronghorn mortalities but attributed only 1 pronghorn mortality to capture, as it was the only one to occur within 3 weeks of capture (Reinking et al. 2019). We recorded no mortalities of feral horses.

During the sage-grouse breeding season, feral horses selected for lower proportions of sagebrush cover (β = -2.02, 95% CI = -3.21, -0.84), less topographically rough areas (β = -1.18, CIs = -1.68, -0.68), and more vegetation biomass (β = 1.16, CIs = 0.46, 1.86) at the 500-m scale along with greater proportions of herbaceous cover (β = 0.16, CIs = 0.01, 0.30) at the 30-m scale, and closer distances to both water sources (β = -1.18, CIs = -1.60, -0.76) and well pads (β = -0.83, CIs = -1.25, -0.41; Fig. 2). Meanwhile, sage-grouse selected for greater vegetation production (β = 0.49, CIs = 0.01, 0.97) and less topographically rough areas (β = -2.11, CIs = -

3.39, -0.83) at the 500-m scale, greater proportion of herbaceous cover (β = 0.31, CIs = 0.13, 0.48) at the 30-m scale and closer distances to well pads β = -1.36, CIs = -2.69, -0.02; Fig. 2). Predicted overlap in occurrence between the species was 0.68 (Fig. 3).

Feral horse and sage-grouse selection were most similar during the summer season as horses selected for lower proportion of sagebrush cover (β = -1.48, CIs = -2.29, -0.68), less topographically rough areas (β = -1.05, CIs = -1.43, -0.66), and greater vegetation biomass (β = 1.20, CIs = 1.03, 2.30) at the 500-m scale along with greater proportion of herbaceous cover (β = 0.33, CIs = 0.20, 0.47) at the 30-m scale, and closer distances to both water sources (β = -0.89, CIs = -1.20, -0.59) and well pads (β = -0.53, CIs = -0.96, -0.11; Fig. 4). Sage-grouse exhibited selection for less topographically rough areas at the 500-m scale (β = -1.63, CIs = -2.76, -0.50), greater proportion of herbaceous cover at the 30-m scale (β = 0.46, CIs = 0.32, 0.60), and closer distances to water (β = -0.82, CIs = -1.32, -0.32; Fig. 4). Predicted overlap in occurrence during the summer season was 0.91 (Fig. 3).

Pronghorn in summer selected for less topographically rough areas (β = -0.83, CIs = -1.17, -0.49) and lower HLI values (β = -0.26, CIs = -0.48, -0.04) at the 500-m scale, with less vegetation biomass (β = -1.38, CIs = -1.86, -0.90), and lower CTI values (β = -0.11, CIs = -0.17, -0.05) at the 30-m scale, and closer distances to water (β = -0.78, CIs = -1.07, -0.49; Fig. 5). Horses selected for greater values of vegetation biomass (β = 0.89, CIs = 0.48, 1.30), less sagebrush cover (β = -1.58, CIs = -2.47, -0.70), and less topographically rough areas (β = -0.98, CIs = -1.36, -0.60) at the 500-m scale, with greater proportion of herbaceous cover (β = 0.25, CIs = 0.12, 0.38), and higher CTI values (β = 0.08, CIs = 0.02, 0.13) at the 30-m scale, and again selected for areas closer to both water (β = -1.08, CIs = -1.44, -0.72) and well pads (β = -0.83, CIs = -1.30, -0.36; Fig. 5). Predicted proportion of occurrence was 0.84 between horses and pronghorn during summer (Fig. 6).

In winter, sage-grouse selected for greater herbaceous cover (β = 0.41, CIs = 0.13, 0.69) and lower HLI values (β = -0.57, CIs = -0.78, -0.35) at the 500-m scale, greater proportion of sagebrush cover (β = 0.83, CIs = 0.67, 0.99) and less topographically rough areas (β = -0.84, CIs = -1.08, -0.60) at the 30-m scale, and closer distances to water (β = -0.44, CIs = -0.66, -0.22) and well pads (β = -2.29, CIs = -3.05, -1.52; Fig. 7). Feral horses exhibited selection for areas that produced greater vegetation biomass in the preceding summer (β = 1.71, CIs = 0.84, 0.26), less sagebrush cover (β = -2.79, CIs = -4.35, -1.23), and less rough topography (β = -1.50, CIs = -2.06, -0.94) at the 500-m scale, and also selected for areas closer to water (β = -0.48, CIs = -0.77, -0.19; Fig. 7). Lastly, pronghorn exhibited selection for less rough areas (β = -1.58, CIs = -1.89, -1.26), lower sagebrush cover (β = -1.64, CIs = -2.31, -0.98), and areas that produced more vegetation biomass during the previous summer (β = 1.60, CIs = 0.92, 2.27) at the 500-m scale, less herbaceous cover (β = -0.37, CIs = -0.54, -0.19) at the 30-m scale, areas closer to water (β = -0.52, CIs = -0.72, -0.33) but areas farther from well pads (β = 0.46, CIs = 0.23, 0.69; Fig. 7). Predicted occurrence overlap was 0.90 between horses and pronghorn, and 0.62 between horses and sage-grouse during the sage-grouse winter season (Figs. 3 and 6).

DISCUSSION

Identifying when and where to implement management actions is key to any successful management strategy (Sydenham et al. 2020), but due to limited budgets (Garrot and Oli 2013) and legislative restraints (Scasta et al. 2018), this need is even more critical within feral horse management areas. We evaluated resource selection of horses, pronghorn, and sage-grouse within a designated feral horse management area and used the results to predict occurrence and quantify overlap among sympatric species. We found that feral horses used similar resources as pronghorn and sage-grouse, translating into moderately high to high degrees of occurrence overlap, depending on the species and season.

The high degree of occurrence overlap between horses and pronghorn in summer reflected similar selection for smoother topography and proximity to water. Smoother terrain can affect use of both species (Ganskopp and Vavra 1987, Girard et al. 2013), and water availability, especially in arid regions, can influence the distribution of both species (Miller et al. 1983, Crane et al. 1997, Mogart et al. 2005). Pronghorn selection for closer proximity to water contradicts earlier work of pronghorn selection during the growing season at the movement scale (Chapter 4). We suggest that this can be explained by the longer time frame and inclusion of the hottest and driest months of the year (July/August). We observed disparate selection between horses and pronghorn regarding vegetation production. As anticipated, given their cecal digestion strategy (Janis 1976; Chapter 4), horses selected for areas with greater aboveground vegetation production, but pronghorn displayed avoidance of these areas during summer. This was an unexpected finding because pronghorn in an adjacent study area displayed selection for greater vegetation production (Reinking et al. 2019), and like distance to water, it is contrary to our movement-scale selection results (Chapter 4). Pronghorn in the Adobe Town HMA appeared to be selecting for more productive areas at a landscape scale but using less productive areas at a finer resolution. These results could indicate resource or space partitioning (Schoener 1974, Macandza et al. 2012) between pronghorn and horses; however, competition may also be a factor. Interference competition between horses and pronghorn has been observed at water (e.g., Gooch et al. 2017; Hall et al. 2017), but competition has not been studied within foraging arenas.

Despite differences in gut morphology (cecal vs. rumen digestion) and feeding strategies (bulk grazer vs. concentrate feeder), diet overlap may be higher than expected between these species, as horse diets have been reported to contain >30% browse in harsh winters or in systems with scant herbaceous production (Stephenson et al. 1985, Krysl et al. 1984). Fecal analyses of horses within the Adobe Town HMA detail a high shrub component in feral horse diets, up to 92.5% in winter (BLM Rawlins Field Office, unpublished report). Further, state game biologists have speculated about competition with horses as a reason why this pronghorn herd has continually failed to meet population targets (WGFD 2017). We stress that our study was not designed to evaluate competition; thus, our results only suggest the need for such research.

Both pronghorn and horses selected areas with less sagebrush cover at the 500-m scale in summer and winter, though confidence intervals overlapped 0 for pronghorn in summer. Both species have shown mixed responses to sagebrush cover (Crane et al. 1997, Miller et al. 1993, Christie et al. 2017, Boccadori et al. 2008), but most studies indicate positive selection for sagebrush cover in winter by pronghorn (Beckmann et al. 2012, Reinking et al. 2019). We offer two reasonable explanations for our results. The findings may be a relic of our sampling design. as the interior of the Adobe Town HMA was characterized by a mixed-shrub community, and areas containing greater proportions of sagebrush were most common at the edges of the study area. Consequently, most study individuals did not reside in areas with high sagebrush cover at a landscape scale. Our results may also indicate that neither species is reliant upon sagebrush to meet seasonal requirements. Selection for sagebrush by pronghorn within regions such as the greater Wyoming Basin could be due to sagebrush being the most dominant shrub species present. Pronghorn densities are highest in sagebrush-dominated systems, but they also inhabit multiple ecoregions and can possess broad diets (Schwartz and Nagy 1976, Hoskinson and Tester 1980; Jakes 2021) suggesting flexibility in resource use.

Contrastingly, sage-grouse displayed selection for sagebrush cover during the winter period, an expected result given that sagebrush makes up the near entirety of their winter diet (Remington and Braun 1985). Though our results also indicated sage-grouse selection for sagebrush during the breeding season, 95% confidence intervals included 0 indicating less importance during this season. This contrasts with sage-grouse breeding habitat selection in other portions of their range where sagebrush cover has routinely been selected for (e.g. Doherty et al. 2010a, Fedy et al. 2014. Kirol et al. 2015). As we indicated earlier, most of this area is not heavily dominated by big sagebrush; instead, it supports a variety of large-statured shrubs that may serve as adequate substitutes for nesting and escape cover. Nest-site selection and nest success in Adobe Town have yet to be quantified, however.

Predicted occurrence overlap between grouse and horses was greatest in the summer, which coincides with the brood-rearing stage for female sage-grouse. Similar to other studies, we found positive sage-grouse selection for areas closer to water and greater proportions of herbaceous cover. Sage-grouse are less reliant on sagebrush during this period (Hagen et al. 2007) and more dependent on taller grasses for cover. Further, forbs and insects constitute a high proportion of chick diets, and both resources are commonly found near water (Crawford et al. 2004). As cecal digesting, bulk roughage feeders, horses require high amounts of herbaceous forage and are dependent on free-standing water (Janis 1976; Chapter 4), meaning that horses present the greatest threat to sage-grouse populations during the summer season in this area.

Several results of winter resource selection among all three species were unexpected. First, distance to water was a strong predictor for each species during winter, even though most surface water was unavailable during this time. We predicted that horses may show selection for areas closer to water solely due to their relatively stable home ranges (Chapter 4), but we expected to find no selection for the other species. Relative strength of selection in winter was weaker for all species compared to other seasons, and coefficient values were strikingly similar across species; therefore distance to water may be correlated with an unknown variable influencing selection during this season. Similar to other studies, pronghorn avoided areas closer to well pads in winter (Beckmann et al. 2012, Reinking et al. 2019); but, selection for these anthropogenic disturbances by sage-grouse was surprising as these features are usually strongly avoided (e.g., Naugle et al. 2011, Holloran et al. 2015). We surmised that distance to well pads may be correlated with sagebrush cover or less topographic roughness, yet neither variable was linked with distance to well pads (r = -0.17 and r = 0.09, respectively), leaving us without an explanation for this result. We hesitate to say that sage-grouse were actively selecting for areas closer to well pads in winter, so we recommend further research to clarify this result. Selection of areas closer to well pads by horses during the sage-grouse breeding and summer seasons were also unforeseen results. We know of no studies that have evaluated responses of feral horses to these features, so we can only speculate that this response may be due to forage availability because invasive grasses and forbs are commonly found near well pads and adjacent roads (Bergquist et al. 2007, Manier et al. 2014). Nonetheless, it appears that horses may not be as sensitive to anthropogenic disturbance as many other wildlife species.

Increased feral horse use in this area has been linked with greater proportions of bare ground and lower mean grass heights (Hennig et al. in review). Consequently, there is real concern regarding the potential for horses to decrease habitat quality for wildlife, especially sage-grouse. Our work can direct the placement of management actions, but we caution that our results should not be interpreted as indications of habitat quality or even population densities for any species. Further, links between horse-related impacts and fitness metrics of co-occurring species have yet to be evaluated, but are essential to fully comprehend the influence of feral horses on sympatric wildlife in the western U.S.

MANAGEMENT IMPLICATIONS

To determine where management actions may be most effective to mitigate potential deleterious effects of horses on wildlife, we recommend examination of resource selection by horses and species of interest within each BLM Herd Management Area or Forest Service Wild Horse and Burro Territory (WHBT). Due to the importance of water for all species in arid regions, we recommend wildlife-friendly fencing (i.e., smooth bottom wires >45 cm from ground level; Jones 2020) around some reservoirs and/or riparian areas within management areas to limit or deter horse-use. This would decrease the degree of horse interference with pronghorn at water and promote growth of herbaceous cover critical to brood-rearing sage-grouse. Further, as horse populations continue to increase, we recommend regular monitoring of breeding success and winter survival of pronghorn and sage-grouse within HMAs and WHBTs. If links between horses and decreased fitness of these species are found, this may warrant horse population control through removal gathers, even in areas that are within appropriate management levels.

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TABLES & FIGURES

Table 1. Justification of explanatory spatial variables for modeling resource selection for feral horses (2017–2019), pronghorn (2017–2019), and greater sage-grouse (2018–2021) within the Adobe Town Herd Management Area, Wyoming USA.

	Justification citation		
Variable	**Horses**	**Pronghorn**	**Sage-grouse**
Percent sagebrush	Miller 1983	Beckmann et al. 2012	Smith et al. 2016
Percent shrub	Miller 1983	Boccadori et al. 2008	
Percent herbaceous	Ganskopp & Vavra 1986	Boccadori et al. 2008	Fedy et al. 2014
Percent bare ground		Christie et al. 2017	
Distance to water	Miller 1983	Deblinger and Allredge 1991	
Distance to well pad		Beckmann et al. 2012	Doherty et al. 2010b
Time-integrated soil-adjusted vegetation index (SAVI)		Christie et al. 2017	Aldridge & Boyce 2007
Topographic ruggedness index (TRI)	Ganskopp & Vavra 1987		Fedy et al. 2014
Compound topographic index (CTI)			Dinkins et al. 2014
Heat load index (HLI)		Reinking et al. 2019	
Slope position	Ganskopp & Vavra 1987		

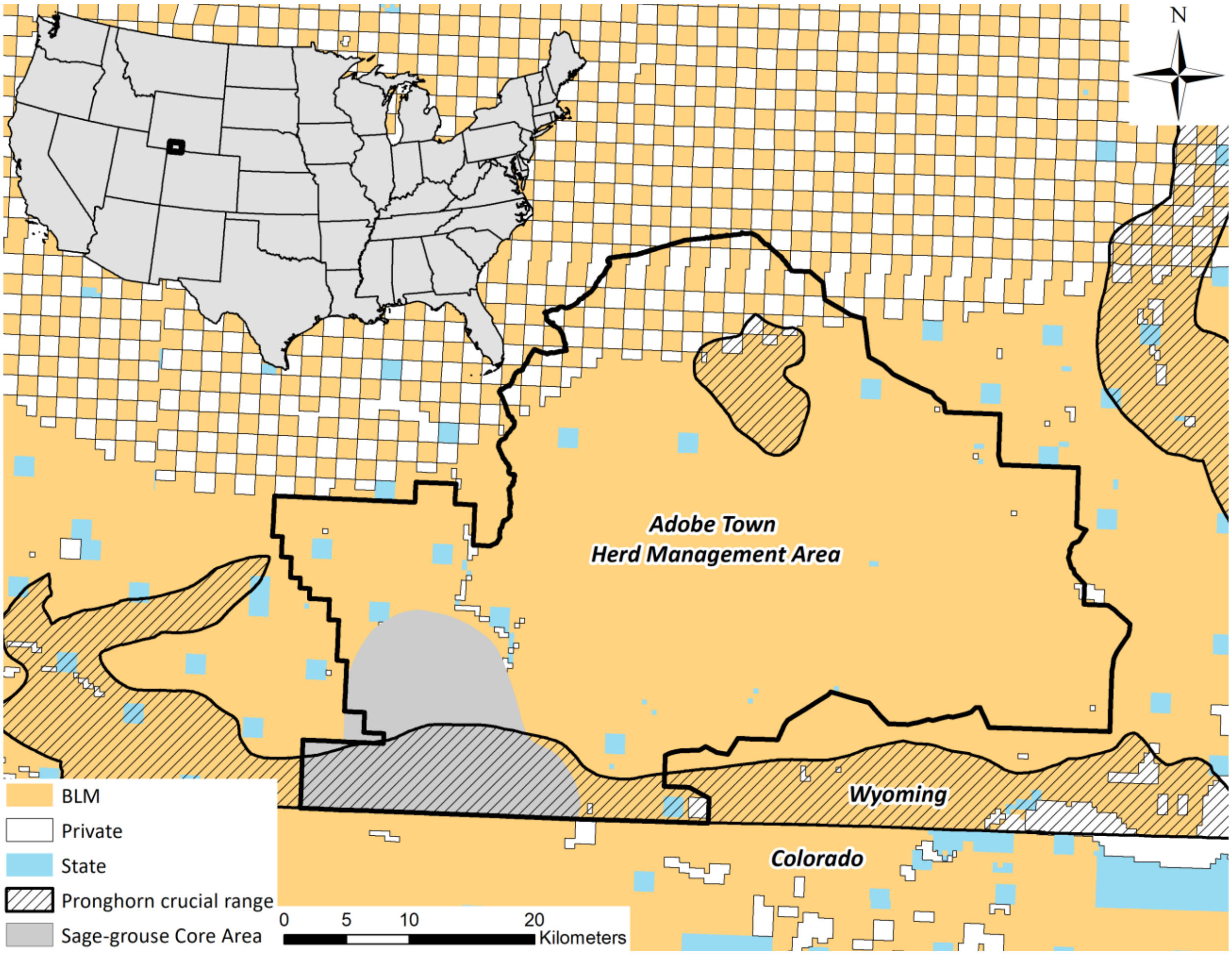

Figure 5.1. Location and surface land management of study area, which included the Adobe Town Bureau of Land Management Herd Management Area, pronghorn yearlong and winter crucial range, and the Powder greater sage-grouse Core Area.

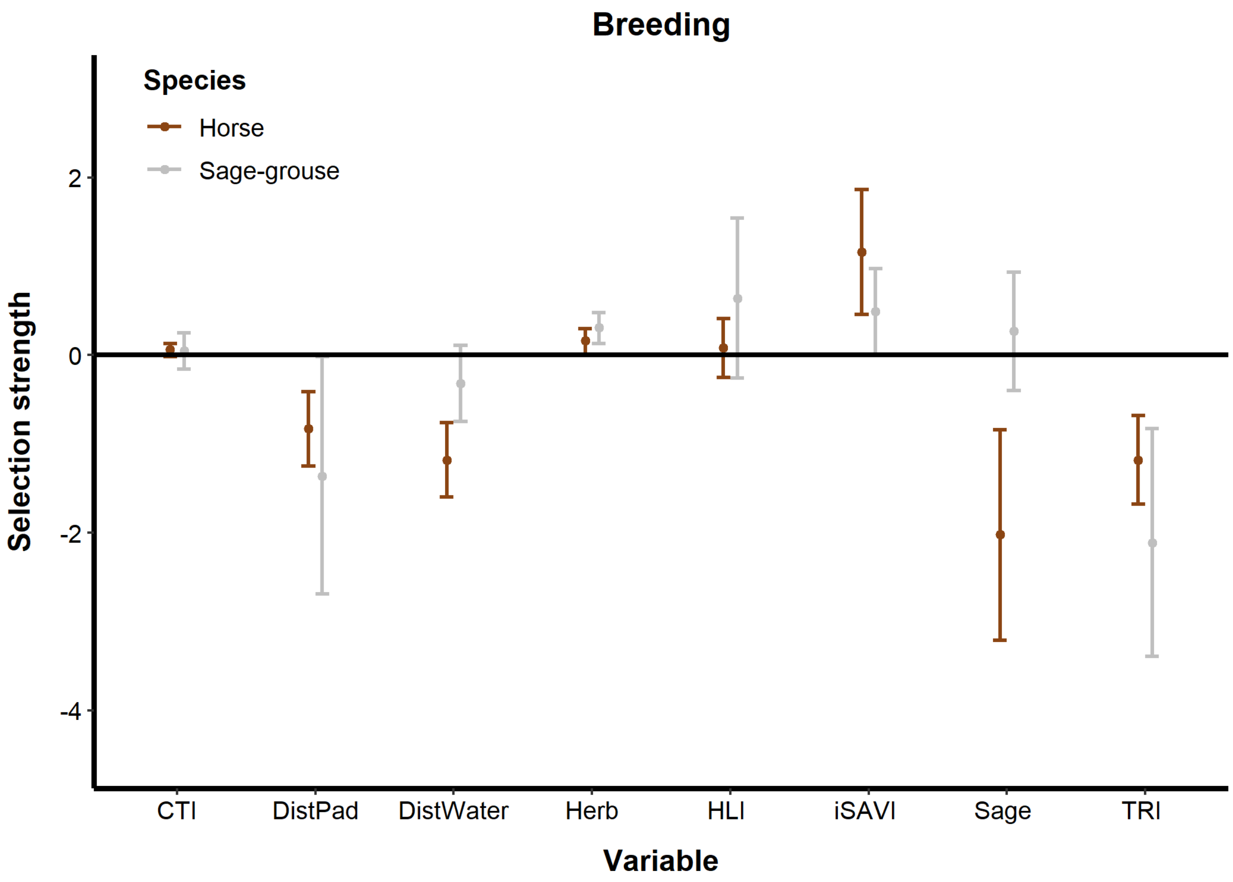

Figure 5.2. Relative strength of selection coefficients and 95% confidence intervals for resource selection by feral horses (2017–2019) and greater sage-grouse (2018–2020) during the greater-sage grouse breeding season (April–June), Red Desert, Wyoming, USA.

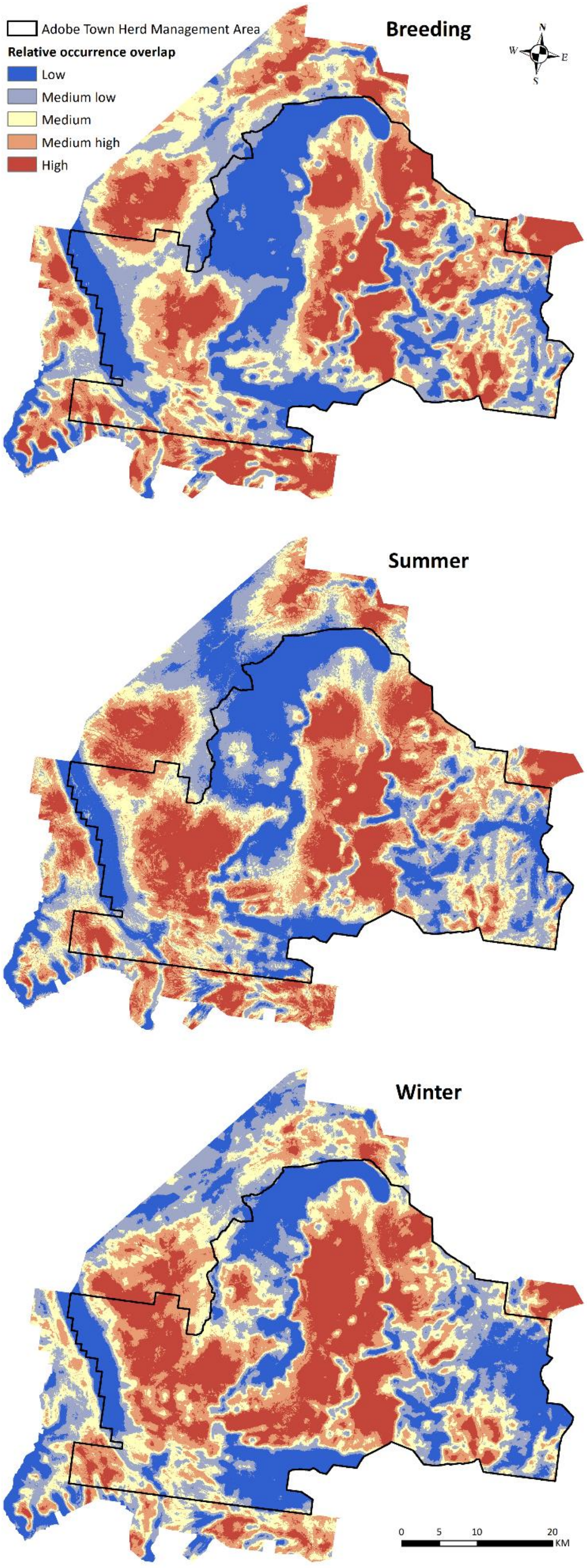

Figure 5.3. Predicted proportion of overlap in occurrence between feral horses (2017–2019) and greater sage-grouse during sage-grouse breeding, summer, and winter seasons (2018–2021), Adobe Town Herd Management Area, Wyoming, USA. This map spatially depicts proportion of overlap binned into five quantiles of relative overlap in occurrence.

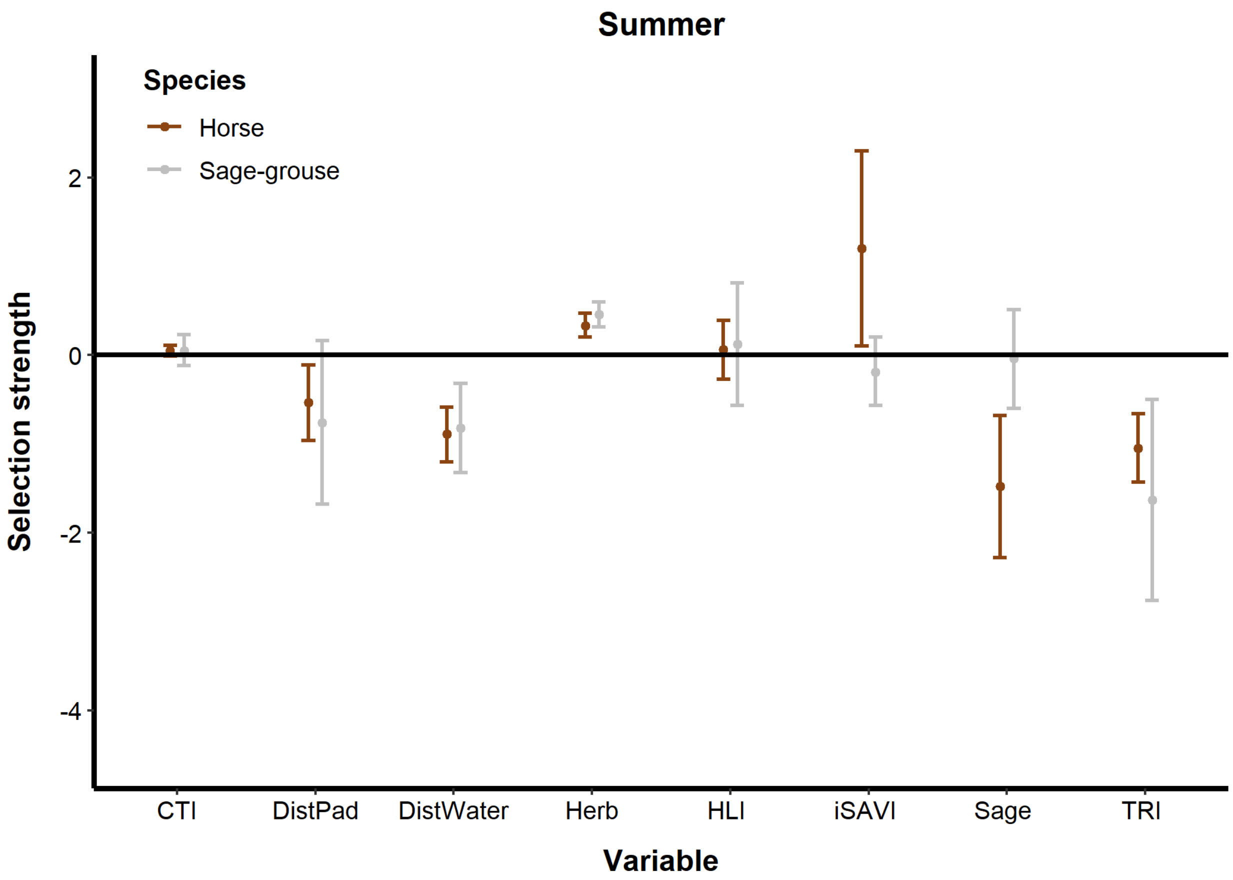

Figure 5.4. Relative strength of selection coefficients and 95% confidence intervals for resource selection by feral horses (2017–2019) and greater sage-grouse (2018–2020) during the greater-sage grouse summer season (July–October), Red Desert, Wyoming, USA.

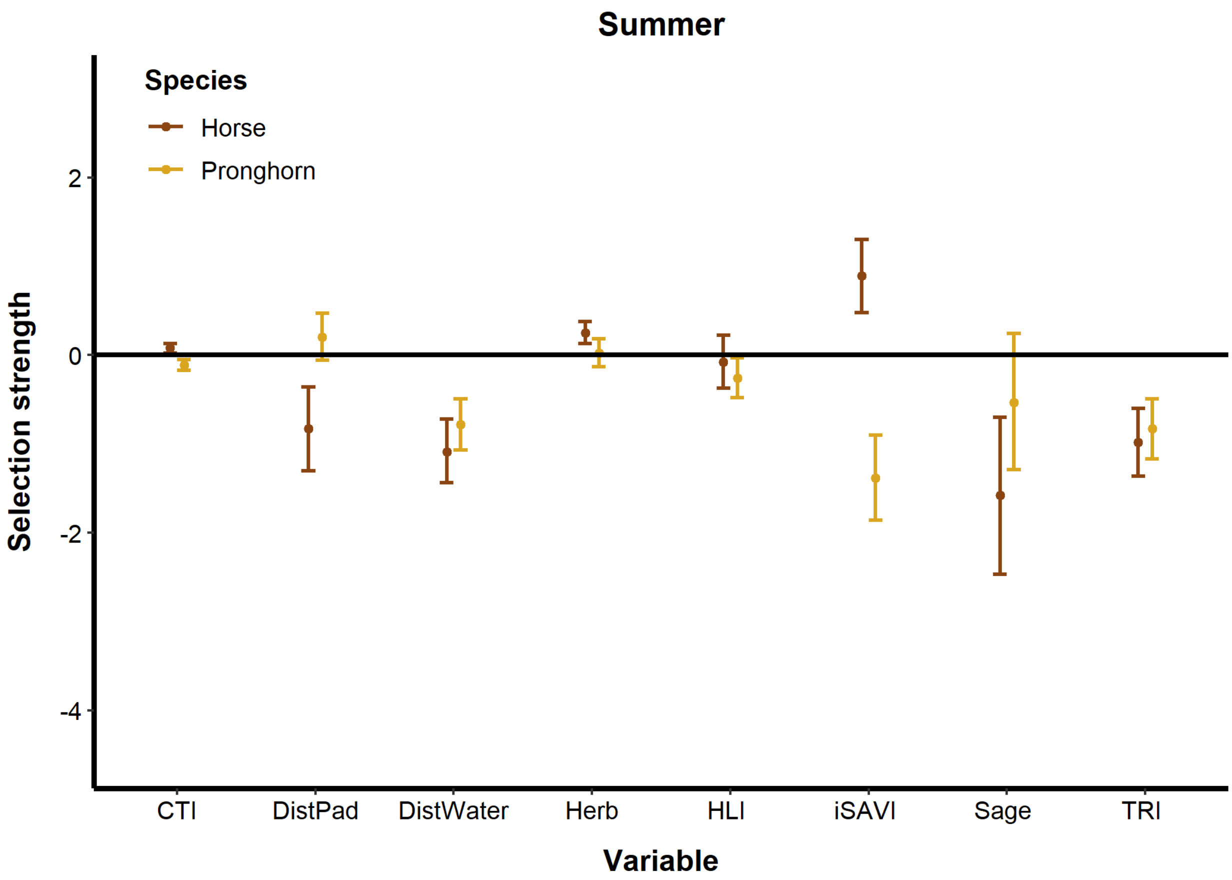

Figure 5.5. Relative strength of selection coefficients and 95% confidence intervals for resource selection by feral horses and pronghorn during summer (April–August 2017–2019), Red Desert, Wyoming, USA.

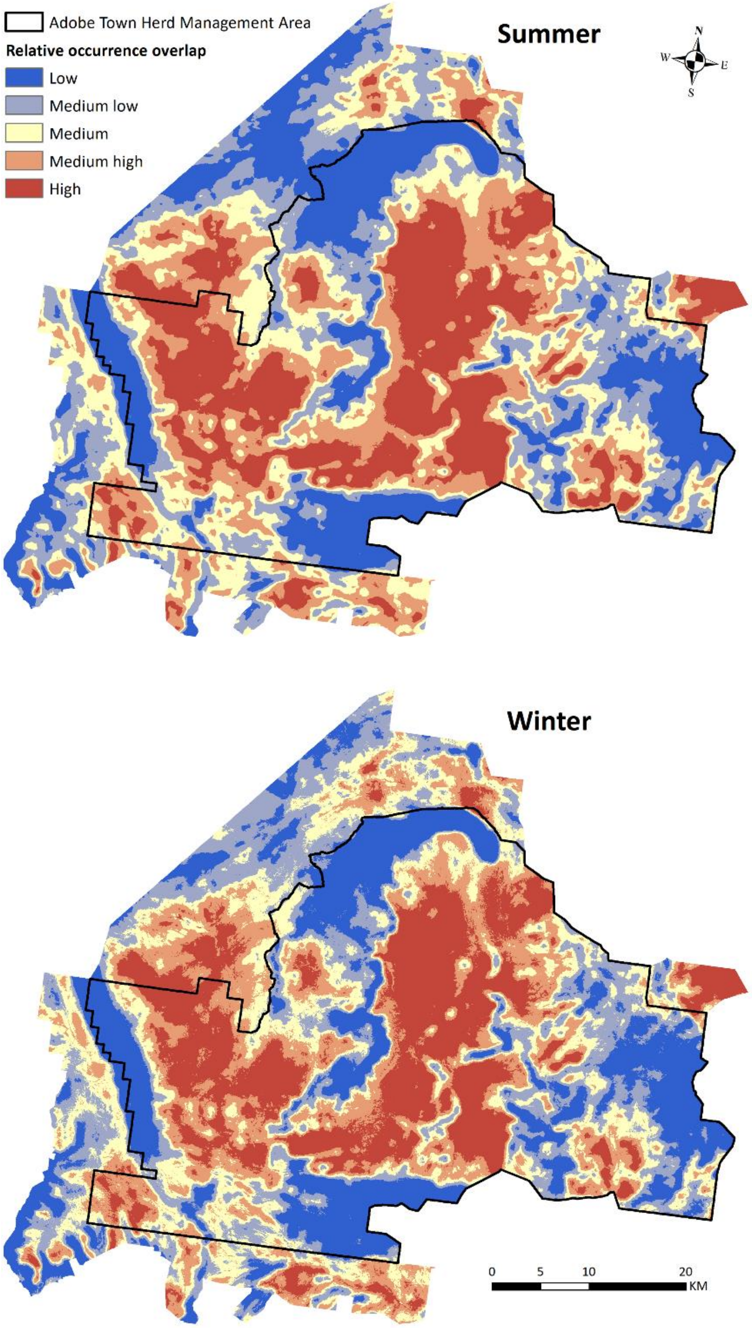

Figure 5.6. Predicted proportion of overlap in occurrence between feral horses and pronghorn during the summer and winter seasons (2017–2019), Adobe Town Herd Management Area, Wyoming, USA. This map spatially depicts proportion of overlap binned into five quantiles of relative overlap in

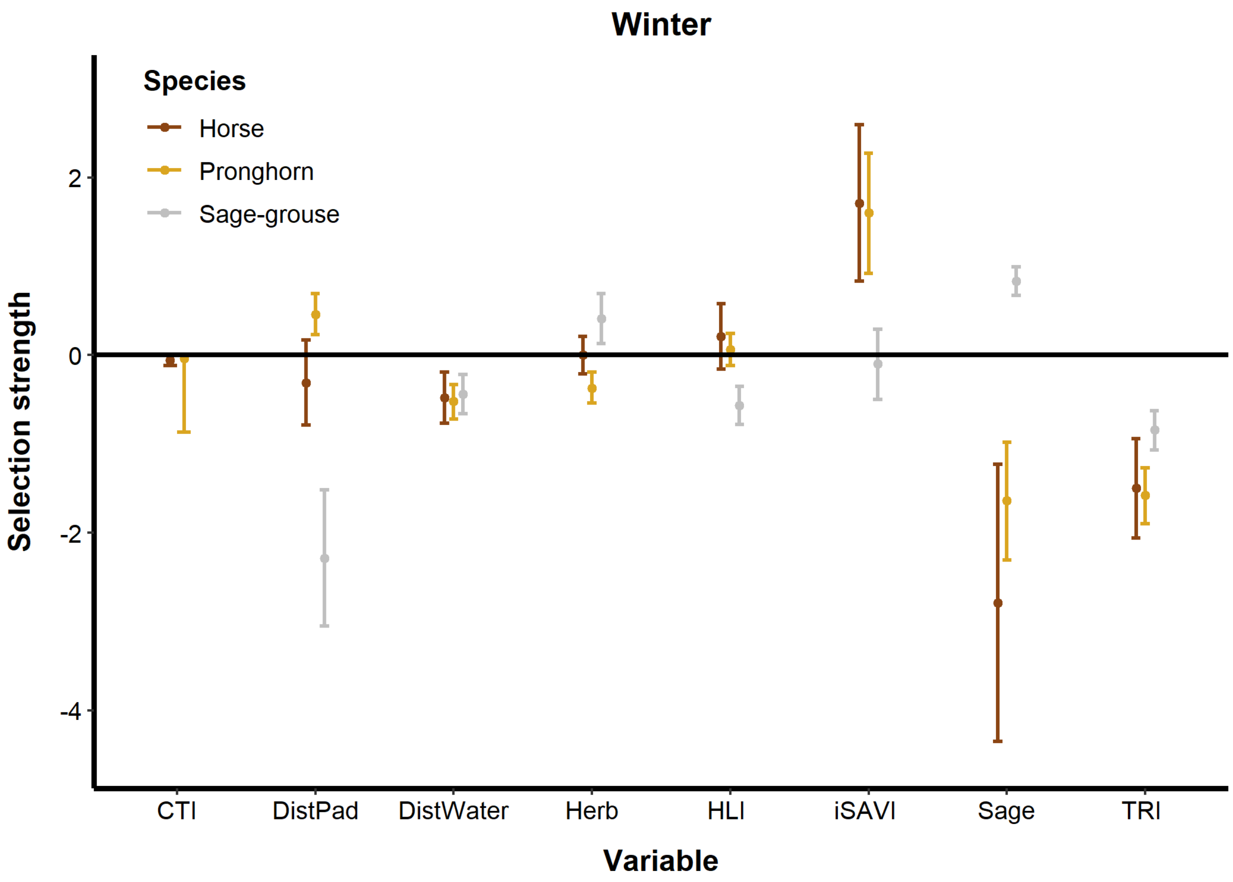

Figure 5.7. Relative strength of selection coefficients and 95% confidence intervals for resource selection by feral horses (2017–2019), pronghorn (2017–2019), and greater sage-grouse (2018–2021) during winter (November–March), Red Desert, Wyoming, USA.