

## Feral horses and pronghorn: a test of the forage maturation hypothesis in an arid shrubland



Jacob D. Hennig<sup>\*</sup>, Jeffrey L. Beck, J. Derek Scasta

Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY, U.S.A.

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Ecologists strive for laws that explain interactions between organisms. Myriad hypotheses have been fundamental in increasing our understanding of plant–herbivore interactions, including the forage maturation hypothesis (FMH). The FMH has recently been extended to include contingencies of body size and digestive system: selection for greater energy potential should be negatively correlated with body mass and selection for proximity to surface water should be greater for hindgut fermenters compared to foregut fermenters or ruminants. While these general trends hold at a broad scale, intrapopulation variability still exists. For feral species that did not coevolve within their current ecological context, variability in habitat selection among populations may be greater. Consequently, understanding habitat selection of each population is imperative to properly inform management. For the case of feral horses, *Equus ferus caballus*, a large-bodied hindgut fermenter, understanding how they compare in habitat selection to sympatric species is of particular interest due to habitat alteration and potential competition. Across much of their range in western North America, horses are sympatric with the smaller-bodied ruminant pronghorn, *Antilocapra americana*. The two species overlap in space use, but we lack information on how each species selects resources within areas of overlap. Accordingly, we compared habitat selection between these two species during the growing season to understand how each responded to predictions of the FMH and to better guide potential management actions. Horses followed FMH predictions by selecting proximity to surface water and greater forage biomass. Meanwhile, pronghorn did not follow predictions of the FMH; pronghorn selected greater forage biomass but did not select greater energy potential. Both species selected greater herbaceous cover, flatter slopes and farther distances from oil and gas well pads. Our analysis reveals a high degree of selection overlap and underscores the importance of conducting population level studies to best understand how herbivores interact with the unique environments they inhabit. © 2024 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Research has identified a strong conceptual link between ungulate movements and vegetation dynamics (e.g. Debeffe et al., 2017; Drescher et al., 2006; Hebblewhite et al., 2008; Mueller et al., 2008). The forage maturation hypothesis (FMH; Fryxell, 1991) has been particularly instrumental in explaining ungulate movement (Avgar et al., 2013; Boone et al., 2006). Measured as crude protein to fibre 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 fibre 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).

A recent global cross-taxa examination extended the FMH to include contingencies of body size and digestive system (foregut versus hindgut fermentation; Esmaeili et al., 2021). Smaller-bodied ungulates have greater relative metabolic rates than larger-bodied species (Bell, 1971). Selection for potential energy intake, the prediction adherent to the FMH, accordingly increased with smaller body size (Esmaeili et al., 2021). Hindgut fermentation is relatively less efficient in water retention than foregut fermentation, or rumination, because more water must be used in the expelling of waste matter (Janis, 1976). Fittingly, hindgut fermenters consistently selected proximity to surface water compared to the varied response of ruminants (Esmaeili et al., 2021).

Macroecological approaches are useful for developing null expectations of ungulate habitat selection but variability in selection still exists among similar species or even between populations within a species. Case in point, the multiple populations of Przewalski's horse, *Equus ferus przewalskii*, and Mongolian gazelle, *Procapra gutturosa*, included in Esmaeili et al. (2021) exhibited differential responses to potential energy intake and forage

\* Corresponding author.

E-mail address: [jhennig@arizona.edu](mailto:jhennig@arizona.edu) (J. D. Hennig).

biomass. The authors proposed numerous reasons for variation in selection among populations, including movement barriers, population density and human interference (Esmaili et al., 2021). Thus, investigation of population level habitat selection is critical before recommending management or conservation actions.

Examination of population level selection of feral species is critical because they often inhabit ecosystems fundamentally different from those which they originally evolved in. Subsequently, selection may vary between populations depending on the availability and distribution of resources or differences in topography. For instance, feral horses, *Equus ferus caballus*, in North America inhabit coastal barrier islands, montane forests, sagebrush steppe and hot, arid deserts (Ransom & Kaczensky, 2016). Habitat selection studies for feral horses are few, but one population in central Utah, U.S.A. avoided steep slopes while another in a nearby area selected steeper slopes (Schoenecker et al., 2023). The authors concluded that this stark difference was likely due to the topographical disparity among the areas (Schoenecker et al., 2023). Moreover, proximity to water had no effect on habitat selection of feral horses in a montane region of Alberta, Canada (Girard et al., 2013), but it strongly influenced selection of populations inhabiting arid regions of the western United States (Hennig, Scasta, et al., 2023; Schoenecker et al., 2023). Therefore, a robust examination of feral horse habitat selection in each distinct ecosystem is needed for proper management. This is a pressing need because feral horse population sizes are far greater than management agencies deem appropriate to avoid the negative effects associated with overabundant horses (BLM, 2023; Hennig, Duchardt, et al., 2023).

Feral horse grazing can reduce native vegetation biomass, increase invasive species cover, decrease soil stability and alter structure and composition of both riparian and upland sites (Beever et al., 2006; Boyd et al., 2017; Davies et al., 2014). This habitat alteration can have negative effects on sympatric vertebrate species including decreased integrity of small mammal communities and population sizes of greater sage-grouse, *Centrocercus urophasianus* (Beever & Brussard, 2004; Coates et al., 2021). There is emerging evidence of interference competition between feral horses and co-occurring ungulate species (Gooch et al., 2017; Hall et al., 2018; Perry et al., 2015), so an understanding of relative selection between horses and sympatric ungulates is needed. In much of their western range, feral horses overlap with pronghorn, *Antilocapra americana*. Although their ranges overlap, there is limited data on how the two species select habitats and share space in areas where they co-occur.

In a previous study, we found that in cold, arid steppe, the two species exhibit similar habitat selection at the home range scale throughout the year (Hennig, Scasta, et al., 2023). Although the two species shared the same space, we lacked information on finer-scale habitat selection within home ranges. Accordingly, we compared third-order habitat selection, or selection with the home range (Johnson, 1980), during the growing season between sympatric pronghorn and feral horse populations in the Red Desert of southern Wyoming and northern Colorado. Based on the FMH, we expected that pronghorn would select potential energy intake because they are a small-bodied ruminant, while feral horses would select proximity to surface water because they are a large-bodied hindgut fermenter.

## METHODS

### Study Area

Our study site encompassed approximately 5600 km<sup>2</sup> and was 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 a mean elevation of 2080 m (USGS,

2016). This area exhibited vegetation phenology typical of a mid-latitude cold desert with a relatively short spring green-up period and meager vegetation production during the growing season (see Table S1, feral horse, in Esmaili et al., 2021). It was a shrub-dominated system with common species including big sagebrush, *Artemisia tridentata*, Gardner's saltbush, *Atriplex gardnerii*, greasewood, *Sarcobatus vermiculatus*, rubber rabbitbrush, *Ericameria nauseosa*, shadscale, *Atriplex confertifolia*, and yellow rabbitbrush, *Chrysothamnus viscidiflorus*. Herbaceous species mainly included perennial grasses such as inland saltgrass, *Distichlis spicata*, prairie junegrass, *Koeleria macrantha*, Sandberg bluegrass, *Poa secunda*, sandhill muhly, *Muhlenbergia pungens*, and squirreltail, *Elymus elymoides*. Natural water sources (i.e. springs and seeps) were rare, but anthropogenic structures, including dirt tanks and stream-fed reservoirs, were installed to improve feral horse distribution and benefit livestock and wildlife populations (M. Astle, U.S. Bureau of Land Management, personal communication).

### Animal Location Data

We deployed global positioning system (GPS) collars on adult female horses and pronghorn within the study area in 2017. We equipped 14 horses with Lotek Wireless IridiumTrackM 3D collars (Lotek Wireless Inc., Newmarket, ON, Canada) between February and March. We later equipped 23 additional horses with Lotek 3D collars ( $N = 8$ ) and Vertex Lite GPS collars (Vectronic Aerospace GmbH, Berlin, Germany;  $N = 15$ ) in October. Horse collars were programmed to record locations every 2 h and remotely detach after 2 years. We captured 35 pronghorn with helicopter net-gunning (Native Range Capture Services, Ventura, CA, U.S.A.) and attached store-on-board GPS/VHF collars (model G2110D; Advanced Telemetry Systems, Isanti, MN, U.S.A.) in November 2017. We programmed transmitters to record locations every 4 h and remotely detach after a 2-year period.

### Ethical Note

Animal handling and use followed protocols approved by the University of Wyoming Institutional Animal Care and Use Committee (protocols 20160826DS00249-01, protocols 20171103DS00295-01, 20190802DS00385-01). At no time were >30 individual horses concurrently equipped with GPS collars, adhering to criteria set forth in the environmental assessment (BLM, 2016). We captured and monitored pronghorn in accordance with protocols approved by the Wyoming Game and Fish Department (Chapter 33 permit: 33-1144). Horses were captured via bait-trapping and helicopter gathers and transported to holding pens for collar attachment. We fitted collars while animals were restrained in a hydraulic squeeze chute and observed animals for  $\geq 48$  h to ensure that collars were fitted properly and not visibly affecting behaviour. To determine quality of collar fit after release, we conducted monthly welfare checks and remotely dropped collars if they were found to be in a precarious position (i.e. over the ears). To reduce pronghorn stress during capture, the processing crew blindfolded, hobbled and fitted collars to individuals at the capture location rather than transport them to a staging area. We recorded 15 mortalities of collared pronghorn during the study time frame, but we classified only one mortality as captured-related (i.e. occurring within 3 weeks of capture date; Reinking et al., 2018). We recorded no mortalities of horses.

### Habitat Variables

Our habitat variables included slope, proportion of herbaceous cover, proportion of shrub cover, mean shrub height, distance to oil or gas well pad, distance to surface water, potential energy intake

and forage biomass (Table 1). We selected these variables based on our previous work (Hennig, Scasta, et al., 2023) and our knowledge of these species and the study area. We calculated slope from a 1/3 arc-second digital elevation model (USGS, 2016) using the ArcGIS geomorphometry and gradient toolbox (Evans, Oakleaf, Cushman, & Theobald, 2014) within ArcMap 10.6 (Esri, Redlands, CA, U.S.A.). We used the National Land Cover Database 2016 shrubland fractional components for the western United States (Rigge et al., 2020) to obtain proportions of herbaceous and shrub cover along with mean shrub height.

A complete record of surface water sources was unavailable, so we used 2017 National Agriculture Imagery Program (USDA, 2017) 1 m images to digitize dirt tanks and reservoirs within the study area. We then added known locations of springs and seeps (M. D. Astle, BLM Rawlins Field Office, personal communication) to the reservoir layer. Because not all digitized water tanks held water each year, we used the movements of telemetered individuals to better assess which sources held water during our study period. We used the 'recurse' package (Bracis et al., 2018) to detect which sources were revisited at least once by an individual horse or pronghorn during our study period. We used a 500 m radius for this analysis because this approximated the combined median step lengths for both populations. We retained all water sources that were revisited at least once by any individual during the study duration and discarded sources that were never revisited.

To estimate forage biomass and potential energy intake, we used MODIS MOD09A1 (250 m spatial resolution, 8-day temporal resolution) scenes to calculate the modified soil-adjusted vegetation index (MSAVI; Qi et al., 1994). This metric is analogous to normalized difference in vegetation index (NDVI) but is a preferable metric for arid rangelands because it better accounts for the reflectance of bare soil (Qi et al., 1994). We followed previous methods to smooth yearly MSAVI time series by first setting all negative values and all pixels classified as clouds, shadow or snow to null values, filling remaining null values through linear interpolation and applying a 3-pixel median filter (e.g. Bischof et al., 2012; Branco et al., 2019; Esmaili et al., 2021; Merkle et al., 2016). We then linearly interpolated between successive 8-day scenes to calculate MSAVI for each day of the year. We calculated the rate of change in MSAVI across each 3-day period (Esmaili et al., 2021) to approximate the instantaneous rate of green-up (IRG) per pixel, which reaches a maximum value where the curves of crude protein content and biomass intersect (Bischof et al., 2012; Merkle et al., 2016).

Slope and landcover variables possessed a 30 m native spatial resolution, but we calculated a 100 m moving window for these variables to use in our analyses to accommodate the spatial error inherent in GPS relocations. We kept MSAVI and IRG variables at their native 250 m resolution. For the distance variables, we calculated a decay function to scale distances from 0 to 1, with greater values indicating closer proximity to water locations and well pads. The decay function took the form of  $e^{-d/a}$ , where  $d$  was Euclidean distance and  $a$  was 100 m. We normalized MSAVI and IRG variables between 0 and 1 based on the maximum value per season (Esmaili et al., 2021). To keep the same scale for all variables, we normalized the other habitat covariates between 0 and 1 as well.

### Step-selection Analysis

We used a step-selection analysis within an information-theoretic approach to assess third-order habitat selection. We limited our analyses to between 22 March and 26 June 2018–2019 to coincide with the growing season (Esmaili et al., 2021). For analysis, we rarified the horse location data set (2 h fix rate) to match the fix rate of our pronghorn (4 h) and retained individuals with >540 locations per season (i.e. 3 months of data), which

translated into 44 and 34 pronghorn and horse animal  $\times$  season combinations, respectively. We generated 10 available steps per each used step by sampling step lengths from a gamma distribution and turn angles from a Von mises distribution fitted using observed distributions of each individual's step lengths and turn angles (Fieberg et al., 2021). We then extracted habitat variables at the end location of each step and extracted MSAVI and IRG values corresponding to GPS location dates. We modelled step selection using a mixed effects conditional Poisson model within the 'glmmTMB' package (Brooks et al., 2017) in R statistical software (R Core Team, 2021). We included step length, natural logarithm of step length and cosine of turn angles in all models to minimize bias in the habitat selection coefficients (Avgar et al., 2016; Fieberg et al., 2021). Following the framework of Muff et al. (2020), we included random intercepts and slopes for each animal  $\times$  season combination and assigned a fixed variance of  $10^3$  for stratum-specific intercepts to prevent them from shrinking towards the population mean. Each stratum was the observed end location of a step along with its matched set of randomly generated available locations (Muff et al., 2020).

We used a two-step approach to examine support for the FMH in explaining habitat selection of horses and pronghorn. First, we parameterized a base model for both species containing slope, distance to well pad, proportion of herbaceous cover and mean shrub height. Proportion of shrub cover was removed from consideration in a base model because of high correlation with herbaceous cover ( $|r| > 0.6$ ) and little support based on exploratory analyses. Second, we fitted a set of models to compare relative support of adding distance to water, MSAVI and IRG to the base model. We ranked models using Akaike's information criterion corrected for small samples sizes (AIC<sub>c</sub>; Burnham & Anderson, 2002) and assessed multicollinearity among habitat variables by calculating variance inflation factors and assured that they were always <2.0 (Merkle et al., 2016). We report model coefficients and 95% confidence intervals for variables found within the top-ranked model per species. We considered a variable to be selected or avoided if the 95% confidence intervals around the coefficient estimate did not overlap 0.

## RESULTS

We examined third-order habitat selection using locations from 27 pronghorn and 19 horses. The top model for horses contained distance to water plus vegetation biomass in addition to the base variables while the top model for pronghorn included vegetation biomass (Table 2). Pronghorn and horses both selected flatter slopes, greater distances from well pads, greater herbaceous cover, and greater vegetation production (Fig. 1). Pronghorn selected lower mean shrub heights but horses neither selected nor avoided shrub height (Fig. 1). Horses selected proximity to surface water (Fig. 1) while this variable received little model support for pronghorn (Table 2). Potential energy intake received minimal support for both species with the additive effect of IRG ranking lower than the base model for horses and pronghorn (Table 2).

## DISCUSSION

We compared third-order habitat selection of sympatric feral horse and pronghorn populations in an arid shrubland. Pronghorn deviated from predictions under the FMH by not selecting greater energy potential and instead selecting greater forage biomass. Horses followed predictions under FMH by selecting proximity to water and forage biomass but not energy potential. Null hypotheses are critical for advancing theory and setting expectations, but our analysis underscores the utility of conducting population level

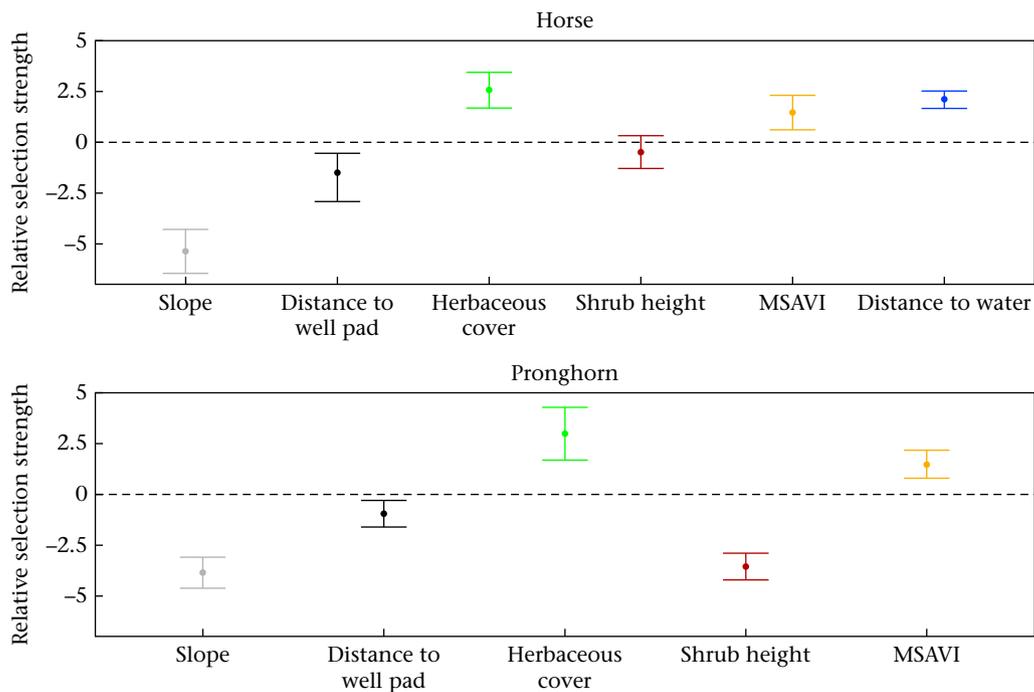
**Table 1**  
Native resolution, analysis scale, and sources for variables in used in step-selection analyses, feral horses and pronghorn, 22 March through 26 June 2018–2019, Red Desert, Wyoming and Colorado, U.S.A.

| Variable  | Native resolution (m) | Analysis scale (m) | Source                     |
|---|-----------------------|--------------------|----------------------------|
| Slope   | 30                    | 100                | USGS (2016)                |
| Proportion of herbaceous cover                  | 30                    | 100                | Rigge et al. (2020)        |
| Proportion of shrub cover                       | 30                    | 100                | Rigge et al. (2020)        |
| Mean shrub height                               | 30                    | 100                | Rigge et al. (2020)        |
| Distance to surface water                       | 30                    | 100                | USDA (2017)                |
| Distance to oil/gas well pad                    | 30                    | 100                | COGCC (2020); WOGCC (2020) |
| Instantaneous rate of green-up (IRG)            | 250                   | 250                | MODIS MOD09A1              |
| Modified soil-adjusted vegetation index (MSAVI) | 250                   | 250                | MODIS MOD09A1              |

**Table 2**  
Model selection information for step-selection functions of feral horses and pronghorn, 22 March through 26 June 2018–2019, Red Desert, Wyoming and Colorado, U.S.A.

| Model                           | K  | AIC <sub>c</sub> | ΔAIC <sub>c</sub> | w <sub>i</sub> |
|---------------------------------|----|------------------|-------------------|----------------|
| <b>Horses</b>                   |    |                  |                   |                |
| MSAVI + Distance to water       | 15 | 394351.9         | 0.00              | 0.85           |
| MSAVI + IRG + Distance to water | 17 | 394355.3         | 3.42              | 0.15           |
| Distance to water               | 13 | 394471.0         | 119.10            | 0.00           |
| Distance to water + IRG         | 15 | 394474.4         | 122.55            | 0.00           |
| MSAVI                           | 13 | 394645.9         | 294.06            | 0.00           |
| MSAVI + IRG                     | 15 | 394649.3         | 297.40            | 0.00           |
| Base model                      | 11 | 394770.3         | 418.39            | 0.00           |
| IRG                             | 13 | 394773.6         | 421.67            | 0.00           |
| <b>Pronghorn</b>                |    |                  |                   |                |
| MSAVI                           | 13 | 437684.1         | 0.00              | 0.70           |
| MSAVI + IRG                     | 15 | 437686.9         | 2.78              | 0.17           |
| MSAVI + Distance to water       | 15 | 437687.9         | 3.80              | 0.10           |
| MSAVI + IRG + Distance to water | 17 | 437690.7         | 6.57              | 0.03           |
| Base model                      | 11 | 437764.8         | 80.73             | 0.00           |
| IRG                             | 13 | 437768.6         | 84.48             | 0.00           |
| Distance to water               | 13 | 437768.7         | 84.60             | 0.00           |
| Distance to water + IRG         | 15 | 437772.4         | 88.34             | 0.00           |

Columns represent the number of parameters (K), Akaike's information criterion adjusted for small sample sizes (AIC<sub>c</sub>), difference in AIC<sub>c</sub> units from top-ranked model (ΔAIC<sub>c</sub>) and model weight (w<sub>i</sub>). IRG = instantaneous rate of green-up; MSAVI = modified soil-adjusted vegetation index.



**Figure 1.** Relative selection strength and 95 % confidence intervals from step-selection functions of feral horses and pronghorn, 22 March through 26 June 2018–2019, Red Desert, Wyoming and Colorado, U.S.A. Dashed line at  $y = 0$  indicates no selection or avoidance. Note that the distance variables are scaled so that a positive values indicate closer proximity to water or oil and gas well pads. MSAVI = modified soil-adjusted vegetation index.

habitat selection assessments to inform management and conservation.

We predicted that as small-bodied concentrate-selecting ruminants, pronghorn would strongly select for IRG (sensu [Esmaili et al., 2021](#)). Indeed, other small to medium-bodied ruminants, such as mule deer, *Odocoileus hemionus*, have exhibited selection for IRG in the western U.S. ([Aikens et al., 2017](#); [Merkle et al., 2016](#)); yet this relationship had not been previously tested for any pronghorn population. Pronghorn are highly selective feeders and this population inhabits an arid system, two characteristics that restrict the applicability of the FMH ([Fryxell, 1991](#)). The FMH was developed in tropical grasslands, but in arid regions with meager herbaceous vegetation production, there is likely little nutritional advantage for ungulates to select small differences in vegetation quality. There is presumably little net energy gain from selecting IRG in this system because greater values may not truly mean greater energy potential. IRG reaches a maximum at an intermediate growth stage, but if there is little forage production from a pixel at peak IRG, another pixel with greater forage production but at a less than optimal growth stage ostensibly provides greater energy. Furthermore, because pronghorn are selective feeders, the scale at which we evaluated potential energy intake (250 m) may be too coarse to be relevant for this species ([Hering et al., 2022](#)).

Our vegetation production metrics were heavily influenced by shrub cover, which may be problematic for our study species because horse diet mainly consists of graminoids while pronghorn can consume a large proportion of forbs, especially during the growing season ([Bleke et al., 2023](#); [McInnis & Vavra, 1987](#); [Scasta et al., 2016](#)). Although our analytical approach should correlate with growing season of herbaceous materials, it may not adequately represent forage to the ungulates in question ([Esmaili et al., 2021](#)). Therefore, remotely sensed indices of forage quality and quantity may not be appropriate for herbaceous-selecting species in shrubland-dominated ecosystems. Future studies should aim to ground-truth remotely sensed indices if possible. Moreover, remote sensing platforms with a finer spatial resolution (i.e. 10 m) may provide a better test; however, great care must be taken to properly generate forage metrics in heterogeneous environs.

Our analysis allowed us to better understand habitat selection at a fine scale for both species relative to what has been previously published. We know that horses and pronghorn overlap in space use throughout the year in this system ([Hennig, Scasta, et al., 2023](#)); but our step-selection analysis provides evidence that in areas where they overlap spatially, they also select similar resources. We show that both species strongly select greater biomass and herbaceous cover. Our analysis could not determine grass versus forb cover or production however, so this is a need in future investigation. At the home range scale, both species avoided tall shrubs ([Hennig, Scasta, et al., 2023](#)), but within home ranges, only pronghorn selected shorter shrub height. This is likely to increase predator detection and offers some level of spatial nonoverlap from horses.

Horses strongly selected proximity to water, but pronghorn did not. In arid regions, hindgut fermenters receive only a small proportion of their water needs from forage and are thus highly dependent on surface water sources ([Kaczensky et al., 2010](#); [Nandintsetseg et al., 2016](#)). Because feral horse grazing can have negative effects on ecosystems ([Eldridge et al., 2020](#)), water developments were installed in this region to distribute horse use more evenly across the landscape. We posit that managing water levels might allow managers to strategically manipulate the grazing patterns of this horse population. Plants are most succulent during the growing season; thus pronghorn use of free-standing water is usually inversely correlated with forage succulence

([Beale & Smith, 1970](#)). Furthermore, pronghorn possess higher body water content than other ruminants, indicating a lower reliance on water ([Wesley et al., 1970](#)). With climate change projected to decrease the availability of water in the future, man-made surface water catchments may be of even more importance. Greater aridity may mean less succulent vegetation during the summer so pronghorn may have to rely more upon free-standing water in the future. While no evidence of interference competition at water has been found within this region ([Hennig, Beck, Gray, et al., 2021](#)), studies in sites with more limited water availability have indicated competition between horses and pronghorn ([Hall et al., 2018](#)). Thus, managers should monitor water use by both species to ensure that horses are not negatively affecting pronghorn.

Both second-order (i.e. home range selection; [Johnson, 1980](#)) and third-order habitat selection studies indicate a strong degree of overlap between horses and pronghorn ([Hennig, Scasta, et al., 2023](#)). However, competition cannot be inferred because these species presumably partition forage species. Nevertheless, heavy use by horses can reduce forage biomass, induce invasive species spread, compact soil, increase bare ground and limit vegetation regrowth ([Hennig, Beck, Duchardt, et al., 2021](#)). Furthermore, interference competition could limit the ability of pronghorn to access high-quality forage sites if horses are present. Although horses and pronghorn may not directly compete for forage species, horses may still influence forage availability and quality for pronghorn. Research into interactions between these species at foraging arenas is an area for future investigation to better understand the effects of this introduced herbivore on pronghorn populations.

#### Author Contributions

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

#### Data Availability

Data for this study are available from the Movebank Data Repository ([Beck et al., 2022](#): [https://www.movebank.org/cms/webapp?gwt\\_fragment=page=studies,path=study2478177417](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study2478177417); [Scasta et al., 2022](#): [https://www.movebank.org/cms/webapp?gwt\\_fragment=page=studies,path=study2478104452](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study2478104452)).

#### Declarations of Interest

None.

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