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Understanding an ecological tug of war: Disentangling competition between native and domesticated ungulates

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Abstract

Competition is a complex ecological process involving individual and community interactions at ecological and evolutionary time scales. Individuals within and between species can compete through two mechanisms: exploitative and interference competition. These mechanisms often co-occur, making it difficult to develop a mechanistic understanding of competition. We used movement data from 19 GPS-collared white-tailed deer (*Odocoileus virginianus*) associated with an experimental cattle (*Bos taurus*) stocking event to disentangle exploitative from interference competition between deer and cattle. We assumed any effect of exploitative competition on reduced forage availability for deer would not occur immediately, whereas interference competition would occur immediately after cattle stocking, and antagonistic interactions between deer and cattle would alter deer behavior and degrade habitat quality. We evaluated the effects of the experimental stocking event on deer for 30-day intervals before and after the cattle stocking event as this period was assumed to be too short for cattle to reduce deer forage resources through exploitative competition. We assessed the effects of interference competition using the movement metrics of home range size, speed, and resource selection. We used home range size as a proxy for habitat quality, assuming cattle would degrade deer habitat through means other than loss of forage. We used speed and resource selection as indicators of deer behavior. We experimentally stocked cattle at densities ranging from 0 to 15.7 animal units/km^2 to previously destocked pastures. Stocking densities did not influence home range sizes ($\widehat{\beta} = 17.033$, 85% CI: −189.471 to 235.322) of deer. However, as stocking density increased, deer decreased speed ($\widehat{\beta} = -0.014$, 85% CI: −0.020 to −0.008) and increased selection for woody cover ($\widehat{\beta} = 0.047$, 85% CI: 0.031 to 0.063) and sandier soils ($\widehat{\beta} = 0.062$, 85% CI: 0.033 to 0.090). Our results suggest cattle density altered deer behavior and their realized niche within our system. Our results demonstrated mechanisms by which competition with livestock could influence native wildlife populations, which can be used to inform management of multiuse working landscapes.

KEYWORDS
cattle, interspecific competition, livestock, movement, resource selection, white-tailed deer, working landscapes

INTRODUCTION

Competition drives interspecific and intraspecific interactions and can influence ecological processes at the evolutionary scale to individual behavior (Darwin & Leonard, 1859; Elton, 1946; Hutchinson, 1957). The severity of a competitive interaction is governed by the level of niche overlap, the availability of resources, and the behavioral, biological, and morphological characteristics of the individuals involved (Costa-Pereira et al., 2018; Hsu et al., 1981; Persson, 1985). Individuals can directly interact through two mechanisms: interference and exploitative competition (Levine, 1976; Tilman, 1987; Wootton, 1994). Interference competition is the process in which antagonistic behaviors by individuals limit the accessibility of resources by others (Anholt, 1990; Levine, 1976; Ping et al., 2011). Exploitative competition is the process in which individuals' use of a common resource reduces the per capita availability of that resource for use by others (Anholt, 1990; Tilman, 1987; Wootton, 1994). In an era of rapid land-use change, evolving community structure, and expansion of invasive species, understanding competition among herbivores, particularly livestock and native wildlife, is increasingly important.

Early models of competition explored the density-mediated effects on population demographics without focusing on the mechanism (Anholt, 1990; Lotka, 1920; Tilman, 1987; Volterra, 1926); thus, these models offered insight into food web dynamics but lacked fundamental understanding of the processes driving these interactions. Evaluating the relative importance of mechanisms of competition is challenging because they often co-occur in natural systems and have aggregate effects on the subordinate's realized niche (Anholt, 1990; Joncour et al., 2022; Ping et al., 2011; Smallegange et al., 2006). Another difficulty for evaluating competition is that niche partitioning has often occurred between sympatric species prior to the investigation (Connell, 1980; Stewart et al., 2002). Therefore, understanding if the realized niche of a species is influenced by another requires approaches that provide observations of the species in the presence and absence, or across a gradient of densities of the competitors (Finke & Snyder, 2008; Hutchinson, 1957; Hsu et al., 1981; Ping et al., 2011; Smallegange et al., 2006). Furthermore, studies must isolate each mechanism to understand its relative importance to competition (Gallien & Carboni, 2017; Malanson et al., 1992; Monahan & Tingley, 2012; Mooney & Cleland, 2001; Panzacchi et al., 2015).

Evaluating competition between livestock and wildlife might offer an opportunity to evaluate the mechanistic processes of competition. Humans have the capability to manipulate a competitor's densities and presence through livestock management and observe the subsequent effects in a subordinate wildlife's behavior. Furthermore, competition between livestock and wildlife has seen a resurgence in interest with increased global demands for food and livestock products, which often results in land conversion and biodiversity loss (Norris, 2008; Ramankutty et al., 2018; Song et al., 2018; Thornton, 2010). In conservation biology, the land-sharing paradigm suggests that lower intensity agricultural practices can result in abundant wildlife on working landscapes (Chappell et al., 2009; Gilroy et al., 2014). Yet, a mechanistic understanding of how livestock influence wildlife is requisite for the optimization of land-use objectives that balance wildlife conservation and agricultural production.

Cattle (*Bos taurus*) and white-tailed deer (*Odocoileus virginianus*) are economically and culturally important ungulates. This is particularly true in Texas, USA, where the economic value of cattle production accounted for about $12.3 billion in 2017 and the value of deer hunting accounted for about $1.6 billion in 2015 (National Agricultural Statistics Service, 2019; Outlaw et al., 2017). In South Texas, white-tailed deer productivity is dynamic, and understanding limiting factors, such as competition with cattle, is needed for evaluating the land-sharing paradigm and the compatibility of these two species (Cook et al., 1971; DeYoung et al., 2019; Hines et al., 2021; Young et al., 2008). Interactions between cattle and *Odocoileus* sp. tend to conform to the asymmetrical competition hypothesis, in that the larger cattle are dominant in the competitive relationship (Chaikina & Ruckstuhl, 2006; Lawton & Hassell, 1981; Persson, 1985). For example, both mule deer (*Odocoileus hemionus*) and white-tailed deer generally avoid cattle, implying interference competition exists between cattle and deer species (Cooper et al., 2008; Krämer, 1973; Loft et al., 1993; Stewart et al., 2002). The inability of deer to tolerate close interactions with cattle limits the accessibility of resources, and often *Odocoileus* sp. will use rugged terrain and dense brush to avoid cattle (Cooper et al., 2008; Depew, 2005; Kie et al., 1991; Loft et al., 1991, 1993; Owens et al., 1991; Stewart et al., 2002). Mule deer have altered activity patterns in response to cattle, spending more time active and foraging rather than resting (Kie et al., 1991). Greater competitor densities often result in increased movement rates by the subordinate competitor (Fronhofer et al., 2015; Liu et al., 2016); therefore, cattle grazing may increase energetic demands and movement of white-tailed deer.

Under conditions when resources are limited, exploitative competition between cattle and deer may occur (Anholt, 1990; Hsu et al., 1981). Deer and cattle operate on opposing ends of the browser-grazer dietary strategy continuum (Esmaeili et al., 2021; Fulbright & Ortega-S, 2013). However, dietary overlap increases when forage becomes limited due to overgrazing or environmental stochasticity (Chaikina & Ruckstuhl, 2006; Hines et al., 2021; Ortega et al., 1997). Furthermore, cattle, due to their greater absolute dietary demands as the larger ruminant, consume approximately five times more biomass daily than deer, and at a 20% dietary overlap, one mature cow can consume the daily equivalent of forage needed to support one deer for a day (Fulbright & Ortega-S, 2013; Hines et al., 2021).

We attempted to disentangle interference from exploitative competition between cattle and white-tailed deer by conducting a short study where cattle were experimentally stocked at varying densities and measuring the immediate behavioral responses in white-tailed deer. We posited that, with abundant resources and limited dietary overlap, exploitative competition between white-tailed deer and cattle would be minimal immediately after a cattle stocking event (Anholt, 1990; Villemereuil & López-Sepulcre, 2011). Therefore, any changes in white-tailed deer space use and behavior immediately after the stocking event would be due to interference competition with cattle (Amarasekare, 2002; Anholt, 1990). We hypothesize that, due to niche partitioning, white-tailed deer niche space would shift because of interference competition independent of the effects of exploitative competition with cattle. We predicted that cattle would not significantly influence home range sizes of deer, as deer will be able to compensate for interference competition through modifications of behaviors before adjusting total space use. We predicted white-tailed deer would increase their movement rates to avoid cattle under greater stocking densities. We predicted the presence of cattle would also result in increased avoidance of water sources and ranch roads by deer, as these are areas where cattle tend to congregate. We predicted deer would increase use of woody cover and lower quality sites, which occur on sandier soils in this region, due to deer being displaced by cattle.

METHODS

Study area

We conducted our study on the Coloraditas Grazing Research and Demonstration Area (hereafter Coloraditas; 27.049142°N, 98.7735315°W) of the East Foundation's San Antonio Viejo Ranch (Figure 1; Montalvo et al., 2020). The Coloraditas is about 30 km southwest of Hebbronville, Texas, USA, and encompasses 7502 ha of native rangeland divided among 10 pastures. Pastures are delineated by 1.3 m tall net wire fences and have areas ranging from 581 to 991 ha. The Coloraditas is on an ecotone between the Coastal Sand Sheet and South Texas Brush Country ecoregions (Texas Parks and Wildlife Department, 2014). The southeast portion of the Coloraditas is characteristic of the Coastal Sand Sheet, with sandier soils, more open grassland, and scattered mesquite (*Prosopis glandulosa*) brush mottes. The northwestern portion is comprised of South Texas Brush Country, with clay-loam soils and dense thorn brush forest (Figure 2; Natural Resources Conservation Service, 2019). The grasslands of the coastal sand sheet included seacoast bluestem (*Schizachyrium scoparium* var. *littorale*), tanglehead (*Heteropogon contortus*), and purple threeawn (*Aristida purpurea*). The thornbrush forest of the South Texas Brush Country included mesquite, brasil (*Condalia hookeri*), and granjeño (*Celtis pallida*) and buffelgrass (*Cenchrus ciliaris*; Montalvo et al., 2020). The 30-year average for the region was 56.4 cm of precipitation per year; minimum temperatures averaged 8.4°C in the winter (December, January, February) and maximum temperatures averaged 36.8°C in the summer (June, July, August; PRISM Climate Group, 2021). The region is considered semi-arid with most rainfall occurring in May–June and September–October, with moderate amounts falling in July–August, but the rain that falls in summer is the most ecologically important (Fulbright et al., 1990). Coloraditas lacked natural water sources, and livestock ponds and water troughs were the only permanent water features available year-round independent of cattle presence. The deer in the Coloraditas were not managed through hunting or supplemental feeding.

Study design

Capture and collar deployment

In March 2020, we deployed 20 GPS collars (Lotek Newmarket, ON, Canada GPS6000SD) on gestating adult (≥3.5 years old) female white-tailed deer captured throughout the Coloraditas. We focused on gestating

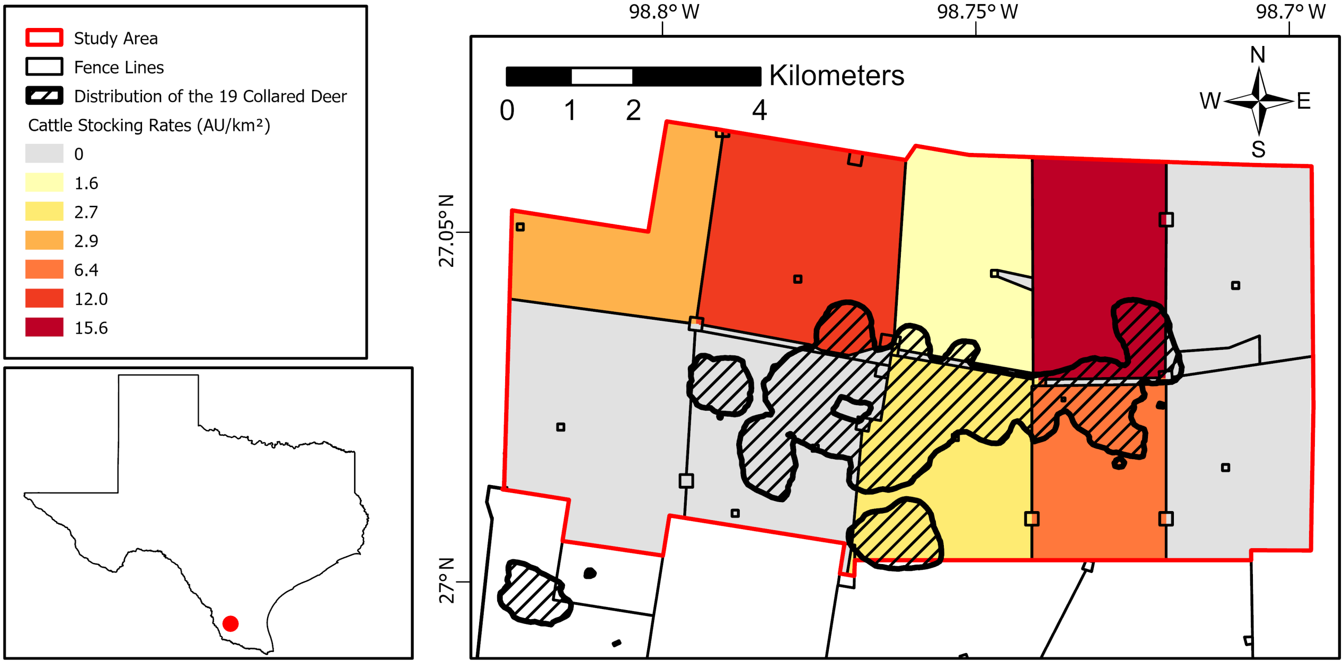

FIGURE 1 The Coloraditas Grazing Research and Demonstration Area, San Antonio Viejo Ranch, Texas, USA, overlaid with the pasture stocking densities following the cattle stocking event on November 2020 and the distribution of collared female white-tailed deer during 6 October–16 December, 2020. The distribution was estimated using the GPS data of the 19 deer whose collars collected data. AU, animal units.

FIGURE 2 Characteristic landscape of the (A) Texas Coastal Sand Sheet and (B) South Texas Brush Country. Photo credit: Calvin Ellis.

females because they represent the group that would most directly link competition to population dynamics and are likely to be in a depleted nutritional state during the cattle stocking event in November due to energetic demands of lactation and therefore would be sensitive to competition (Bender & Hoenes, 2017). We captured deer through aerial net-gunning and restrained netted individuals by hobbling and blindfolding the animals (Webb et al., 2008). We transported deer from their capture locations to a central processing site via a utility terrain vehicle. At the central processing site, we recorded biological measurements, confirmed pregnancy during the second trimester using ultrasonography, and fit gestating deer with a collar. We estimated the age of white-tailed deer using tooth eruption and wear (Foley et al., 2021; Severinghaus, 1949) and programmed collars with a constant fix rate of 3 h (8 fixes/day). We released animals immediately following processing. We recaptured all collared deer one year later in March 2021 to retrieve collar location data. We conducted field trials to determine collar location error, which indicated a GPS error of 7.48 m at the 85th quantile. All deer were captured and handled under the TAMUK IACUC permit 2020-10-19 and in accordance with the American Society of Mammologists guidelines (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists, 2016).

Cattle stocking

To assess the influences of cattle grazing on white-tailed deer space use and behavior, we experimentally stocked cattle in the Coloraditas and evaluated deer movement for the 30 days before (6 October 2020–4 November 2020) and the 30 days after (12 November 2020–11 December 2020) the stocking event. We excluded data during the stocking event (5 November–11 November) to avoid the confounding effects of human activity during cattle stocking. The Coloraditas was previously grazed, but cattle were removed during June 2018 due to poor rangeland conditions brought on by a drought. Over a 6-day period, from 5 to 11 November 2020, we moved cattle into six of the 10 pastures resulting in varying stocking densities between 0 and 15.6 animal units (AU)/km^2 (Figure 1). Cattle remained in the Coloraditas past the duration of the study. A ranch personnel used roads to visit all pastures in the Coloraditas to check cattle once per weekday for a period of about 4–6 h, to verify cattle did not escape designated pastures and water sources remained active. We used program R version 4.2.1 (R Core Team, 2022) and the "raster" package (Hijmans et al., 2022) to create a grid-based spatial representation (i.e., raster; resolution: 15 m) of these stocking densities from pasture shapefiles provided by the East Foundation. We used program R version 4.2.1 (R Core Team, 2022) in all further modeling and data preparation.

Landscape covariates

Habitat productivity for white-tailed deer is often driven by soil characteristics (Dykes et al., 2018; Foley et al., 2018; Lashley et al., 2015; Leopold & Krausman, 1991; Virgós & Tellería, 1998). In South Texas, the proportion of sand within the surface soil horizons can affect vegetation community structure and plant nutritional value (Box, 1959; Zhou et al., 2017). Sandier soils have lower moisture holding capacity resulting in vegetation communities that are poorer quality habitat for white-tailed deer and have been correlated with reduced forb production and body mass in deer (Foley et al., 2018; Fulbright et al., 2021). We derived a geospatial vectorized map of soil types and sand content from the Web Soil Survey (Natural Resources Conservation Service, 2019) to evaluate how white-tailed deer selection of soil texture was altered due to the cattle stocking event. We used the "raster" package (Hijmans et al., 2022) to convert this map into a geospatial raster representing percent sand content with the same extent and resolution of the cattle stocking raster.

Water and roads are often important resources that influence cattle space use and grazing intensity. A non-lactating cow needs to consume 22–57 L of water per day depending on climatic conditions (Lardy et al., 2008), so water can restrict cattle distributions (Leeuw et al., 2001). White-tailed deer, however, are not as spatially restricted by water only requiring between 1.56 and 3.36 L/day to meet their metabolic requirements, much of which may be obtained through dietary moisture (Hewitt, 2011; Webb et al., 2007). Additionally, roads offer ease of travel for livestock and are often utilized by ranchers to feed and monitor animals (Roath & Krueger, 1982). In South Texas, many water sources are artificial and are situated along roadways (Cooper et al., 2008; González et al., 2014; Webb et al., 2007). Therefore, we sourced spatial data for all water and roads from the East Foundation and used the "raster" package (Hijmans et al., 2022) to create continuous Euclidean distance raster layers to both these features.

Deer often make greater use of sites less preferred by cattle such as dense woody vegetation (Cooper et al., 2008; Depew, 2005; Loft et al., 1991). Therefore, we estimated brush cover within our study site from Light Detection and Ranging (LIDAR) data sourced from the Texas Natural Resource Information System (2022). We used the "lidR" package (Roussel & Auty, 2022) to create a vegetation height raster (resolution: 1.5 m) using the methods described by the package creators. We classified this vegetation height raster as either brush or non-brush by first randomly generating 500 points (37 points/km^2) within our study site and extracting vegetation height from the raster cells the points overlayed. Using aerial imagery, we visually assigned these points as either brush or non-brush and then proceeded to use a random selection of 400 of these points to fit a logistic regression model to predict the probability of brush being the predominant cover type of a cell from the vegetation height of a raster cell (Li et al., 2014). We used this model to estimate the probability of brush for the entire vegetation height raster and then assigned cell values as either brush or non-brush using a logistic probability threshold of 0.5. We used the remaining 100 points to evaluate model performance of the classified raster by determining the proportion of misidentifications (Comber et al., 2012; Li et al., 2014). We achieved an acceptable accuracy of 91% and resampled the classified raster to the final resolution of 15 m using the mean of the cell values to estimate the percent cover of brush.

Analysis

Recent theoretical, methodological, and technological advances have allowed for new opportunities to understand the processes of competition (McCallen et al., 2019; Ortega et al., 1997; Smallegange et al., 2006). GPS technology illuminated the spatiotemporal movements of animals, allowing for the examination of how animal behavior changes due to the presence of a potential competitor (Cagnacci et al., 2010; Cooper et al., 2008; Hebblewhite & Haydon, 2010; Petroelje et al., 2021). Animal movement data offer a promising opportunity to evaluate mechanisms of competition. For example, Harestad and Bunnell's (1979) habitat productivity hypothesis linked habitat quality to home range area, predicting that an animal will use the smallest area required to meet its life history requirements. Thus, independent of environmental variation due to seasonal stochastic change and exploitative competition, changes in habitat quality due to interference competition should be reflected in the home range area of an animal. Additionally, interference competition for resources should impact the subordinate's behavior and realized niche and may be measured using speed or resource selection (Leo et al., 2015; Petroelje et al., 2021; Ziv et al., 1993).

Home range

We estimated home range sizes to assess changes in habitat quality for white-tailed deer as a potential consequence of interference competition with cattle. We identified home ranges by estimating utilization distributions (UD) from a dynamic Brownian bridge movement model (DBBMM; Kranstauber et al., 2012). We choose DBBMMs due to their ability to handle autocorrelated movement data and used the "move" package (Kranstauber et al., 2020) to develop the DBBMMs. For each deer, we estimated a UD from the movement data collected 30 days before the stocking event and a UD from the movement data collected 30 days after the stocking event. We estimated home range areas at the 95% isopleth for each UD.

Since deer movement between pastures was not limited during the study, to link home range area estimates to stocking densities, we calculated the average stocking density a deer experienced for each UD. For home range areas estimated after the stocking event, we extracted cattle stocking densities to the GPS data collected after 11 November 2020 and then calculated the average stocking density experienced by each collared deer. We assigned a stocking density of 0 AU/km^2 to all home ranges prior to the stocking event. We used the "lme4" package (Bates et al., 2023) to fit a linear mixed-effect model, where home range area was a function of stocking density and included a random effect for an individual-specific intercept. We identified influential parameters by determining if the 85% CI for a variable excluded zero (Arnold, 2010).

Movement

We estimated speed (in meters per second) to evaluate changes in white-tailed deer behavior due to the presence of cattle. For each collared deer, we estimated the speed between consecutive GPS locations, for those locations collected 30 days before and 30 days after the stocking event. We used the "animal movement tools" package (amt; Singer et al., 2022) to estimate the speed between consecutive GPS points, assigning the value to the origin location. We linked speed estimates to cattle stocking data, by using the "raster" package (Hijmans et al., 2022) to extract stocking densities to the GPS collar data collected after 11 November 2020, while those points collected before the event were assigned the stocking density of 0 AU/km^2. We log-transformed our speed estimates to reduce positive skew in our data before we fitted a linear mixed-effects model using the "lme4" package (Bates et al., 2023). Our model was structured to predict the log-transformed speed estimate as a function of stocking density and a random effect for an individual to account for dependence among observations for the same animal. Models were fitted with all data collected before and after the stocking event. We identified informative parameters in the model by determining if the 85% CI excluded zero (Arnold, 2010).

Resource selection

We assessed how cattle stocking densities influenced deer resource selection by fitting step-selection functions (SSF;

Avgar et al., 2016; Fieberg et al., 2021; Johnson, 1980). An SSF uses a case–control logistical model to evaluate resource selection as the animal moves through the landscape (Avgar et al., 2016; Fortin et al., 2005; Thurfjell et al., 2014). We used the functions contained within the "animal movement tools" package (amt; Singer et al., 2022) to prepare the data to fit the SSFs. For each deer, we paired every actual step with 15 randomly generated steps for the GPS data collected in the 30 days before and after the stocking event. We generated random steps from the individual's step length and turn angle distributions (Avgar et al., 2016; Thurfjell et al., 2014). We then extracted landscape covariates (percent brush cover, percent sand, distance to road, distance to water, and cattle stocking density) to the ending points of both the actual and random steps. We assigned a stocking density of 0 AU/km^2 to the ending points of both the actual and random steps that occurred before the stocking event. We scaled and centered all covariates to aid in convergence and comparison of effects across covariates. We fit three candidate models: a null model with only an intercept, a model containing only the additive effects of the five covariates, and global model with an interaction between stocking densities and the other landscape covariates using the "survival" package (Table 1; Avgar et al., 2016; Fieberg et al., 2021; Therneau et al., 2022). All models included a movement kernel of step-length and turning angle (Avgar et al., 2016), a cluster term to control for individual variation, and a stratification term for the paired random and actual steps. We fitted all models with the full before and after data set, so we could evaluate how deer selection varied after experiencing no cattle on the landscape to encountering a range of stocking rates.

TABLE 1 Ranked step-selection function candidate models used to evaluate how white-tailed deer selection of environmental covariates responded to the cattle stocking event that occurred in November 2020 on the Coloraditas Grazing Research and Demonstration Area, San Antonio Viejo Ranch, Texas, USA.

Model name	Model	ΔAIC
Global	PB + PS + DR + DW + SD + SL + TA + SD*PB + SD*PS + SD*DR + SD*DW	0
Direct effects only	PB + PS + DR + DW + SD + SL + TA	38.63
Null	1 + SL + TA	2216.03

Note: Selection was evaluated for percent brush, percent sand, distance to road, and distance to water.

Abbreviations: AIC, Akaike information criterion; DR, distance to road; DW, distance to water; PB, percent brush; PS, percent sand; SD, stocking density; SL, step length; TA, turn angle.

We used variance inflation factor (VIF) to check for high collinearity (VIF > 5) of our covariates and found none of our explanatory variables exhibited high collinearity. We used Akaike information criterion (AIC) to ascertain our top model and identified informative parameters by determining if a coefficient's 85% CI excluded zero (Akaike, 1973, 1974; Arnold, 2010; Bolker et al., 2009).

RESULTS

Of the 20 GPS collars we deployed, we recovered location data from 19 of the adult female white-tailed deer. One collar failed to collect data, so this individual was excluded from the analysis. Collars collected on average 239 locations before and 239 locations after the cattle stocking event. All 19 deer experienced a stocking density of 0 AU/km^2 prior to the stocking event, and 3 deer were never recorded in a pasture occupied by cattle following the stocking event. Nine deer had GPS locations recorded in two treatment pastures, four deer had GPS locations recorded in three treatment pastures, and two deer had recorded locations in at least four of the treatment pastures. Of the GPS locations recorded after the stocking event, 48% of the locations were recorded in the 2.7 AU/km^2 pasture and 28% of the locations were recorded in a pasture without cattle. The remaining GPS locations were either recorded in the 6.43 AU/km^2 pasture (11%), the 15.6 AU/km^2 pasture (7%), the 12 AU/km^2 pasture (5%), or the 1.61 AU/km^2 pasture (1%). Collared deer experienced an average stocking density ranging between 0 and 14.88 AU/km^2 in the 30-days after the stocking event (Appendix S1: Table S1). One deer shifted its home range to a neighboring unstocked pasture outside the Coloraditas but returned during the 30-day period before the stocking event, resulting in an abnormally large home range area estimate for that individual.

Home range area of white-tailed deer was independent of stocking densities ($\hat{\beta} = 17.033$, 85% CI: −189.471 to 235.322; Figure 3; Appendix S1: Table S2). The average home range area of female white-tailed deer during this study was 86.3 (SE = 7.87) ha and 86.0 (SE = 5.87) ha before and after the cattle stocking event, respectively (Figure 3). In contrast, movement and resource selection of white-tailed deer varied with cattle stocking density (Figures 4 and 5). Speed of white-tailed deer decreased 1.4% ($\hat{\beta} = -0.014$, 85% CI: −0.020 to −0.008; Appendix S1: Table S3) for every 1 AU/km^2 increase in cattle stocking densities (Figure 4). The presence of cattle influenced resource selection of white-tailed deer; the global model with interactions between stocking densities and the other covariates was the best fitting SSF model (Table 1). The global model indicated that a

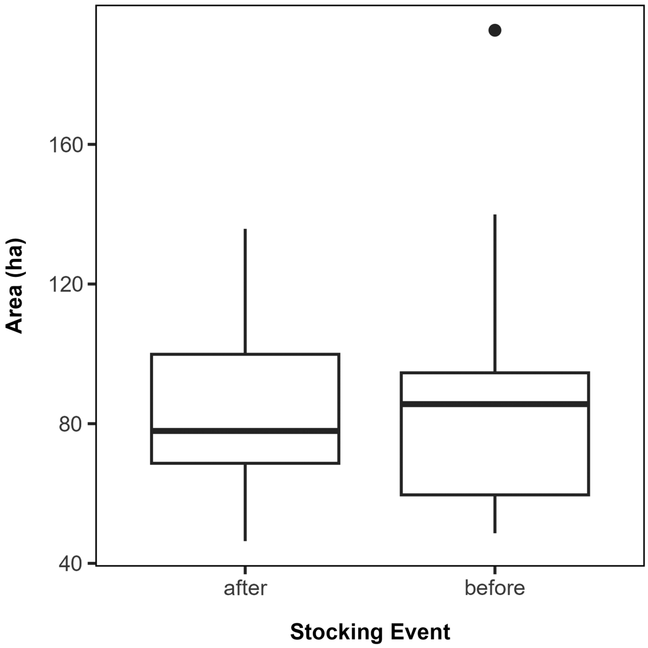

FIGURE 3 Boxplot of the estimated home range areas of the mature female white-tailed deer (n = 19) GPS-collared in the Coloraditas Grazing Research and Demonstration Area of the San Antonio Viejo Ranch, Texas, USA. Home range areas were estimated for 30 days before and for 30 days after a cattle stocking event (November 2020) at the 95% isopleth of a utilization distribution created with dynamic Brownian bridge movement models. Boxplot midlines represent the median, box limits represent the 25th and 75th quantiles, and whiskers represent the minimum and maximum home range area estimates, excluding outliers. Outlier home range area estimates are represented by dots.

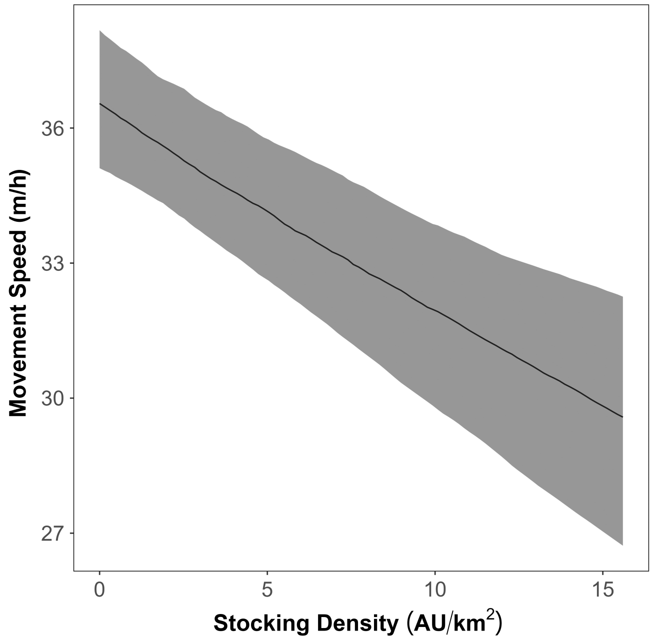

FIGURE 4 Influence of cattle stocking density on speed (in meter per hour) of mature female white-tailed deer (n = 19). Speed was estimated using the GPS data collected in the 30-day periods before and after cattle stocking at the Coloraditas Grazing Research and Demonstration Area, San Antonio Viejo Ranch, Texas, USA, during November 2020. AU, animal units.

1 AU/km^2 increase in stocking densities increased the relative selection strength of percent brush cover by 0.002 ($\widehat{\beta}$ = 0.047, 85% CI: 0.031 to 0.063) and percentage of sand in the surface soil horizon by 0.005 ($\widehat{\beta}$ = 0.062, 85% CI: 0.033 to 0.09, Table 2, Figure 5). White-tailed deer neither selected or avoided water ($\widehat{\beta}$ = 0.017, 85% CI: −0.130 to 0.163, Table 2) or roads ($\widehat{\beta}$ = −0.080, 85% CI: −0.170 to 0.011, Table 2).

DISCUSSION

Our results suggest that interference competition between cattle and white-tailed deer resulted in changes in two of three behavioral metrics, speed, and resource selection. We suspected that exploitative competition between cattle and deer would be minimal immediately after stocking as the Coloraditas had favorable rangeland conditions after being destocked for two years and due to cattle and deer operating on opposing sides of the browser-grazer dietary continuum (Hines et al., 2021; Ortega et al., 1997). Thus, exploitative competition with cattle would not have significant effects on deer space use and behavior (Anholt, 1990; Villemereuil & López-Sepulcre, 2011). Therefore, our study design was effective at exhibiting the effects of interference competition on the shifts in the realized niche of a species mostly independent of the exploitative effects. In the 30 days after cattle were reintroduced to the Coloraditas, cattle influenced white-tailed deer behavior as indicated by reduced movement and increased selection of brush and sandy sites with increasing cattle density. It is probable that a longer study would exhibit further deviation in deer niche space and behavior due to exploitative competitive effects becoming more apparent.

As expected, we found white-tailed deer home ranges were similar before and after the stocking event, indicating deer were able to compensate for interference competition with cattle through other behavioral modifications. Additionally, exploitative competition was likely insignificant because cattle grazing did not significantly reduce forage abundance for white-tailed deer to exhibit a change home range size. Our results differ from previous studies that observed greater home range areas used by deer in response to the presence of cattle grazing (Chaikina & Ruckstuhl, 2006; Hines et al., 2021; Loft et al., 1993). We suspect this divergence in results is due

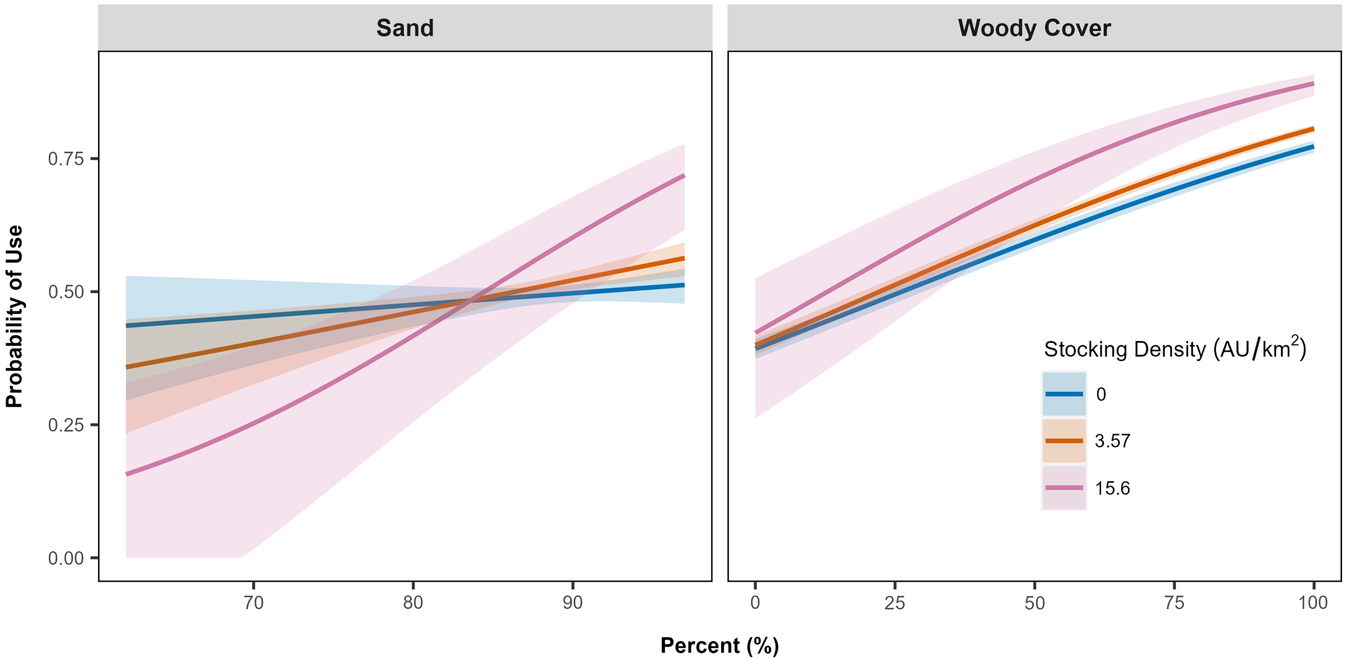

FIGURE 5 The influence of cattle stocking on resource selection (woody cover and percent sand in soil) of adult female white-tailed deer ($n = 19$) when all other covariates held at their respective means. Selection was evaluated using the top performing step-selection function model using data collected in the 30 days before and after cattle stocking in the Coloraditas Grazing Research and Demonstration Area, San Antonio Viejo Ranch, Texas, USA, during November 2020. AU, animal units.

TABLE 2 Step-selection function coefficients and their associated 85% CIs from the top fitting model examining how white-tailed resource selection was altered following the November 2020 cattle stocking event in the Coloraditas Grazing Research and Demonstration Area, San Antonio Viejo Ranch, Texas, USA.

Variable	$\widehat{\beta}$	SE	85% CI
Percent brush	0.473	0.010	0.446 to 0.501
Percent sand	0.067	0.015	0.011 to 0.122
Distance to road	−0.080	0.021	−0.170 to 0.011
Distance to water	0.017	0.028	−0.130 to 0.163
Stocking density	0.071	0.035	−0.050 to 0.192
Step length	0.027	0.011	0.019 to 0.034
Turn angle	−0.014	0.011	−0.033 to 0.005
Stocking density × percent brush	0.047	0.011	0.031 to 0.063
Stocking density × percent sand	0.062	0.016	0.033 to 0.090
Stocking density × distance to road	−0.070	0.021	−0.141 to 0.001
Stocking density × distance to water	0.042	0.026	−0.021 to 0.105

to stronger grazing intensity and longevity of these studies relative to ours. These previous studies observed greater shifts in rangeland conditions due to livestock grazing, and potentially exploitative competition with wildlife would increase with resource scarcity due to grazing (Anholt, 1990; Dickie et al., 2022; Harestad & Bunnel, 1979). The relative importance of exploitative and interference competition over a longer time period in our system is an open and important question. Our goal was to isolate the role of interference competition with cattle in influencing the realized niche of a native ungulate, and therefore, the short time period of our study was useful in revealing this effect.

Counter to our prediction, white-tailed deer speed experienced a modest but consistent decrease with greater stocking densities. We suspected deer would increase their movement to avoid cattle, as general avoidance behavior by mule deer and white-tailed deer is well supported in the literature (Cooper et al., 2008; Kie et al., 1991; Krämer, 1973; Loft et al., 1993). Previous research has indicated that exploitative competition can stimulate increases in movement rates and activity of individuals, as this behavioral modification can assist in acquiring resources (Carbone et al., 2003; Foley et al., 2018; Snaith & Chapman, 2005; Thouless, 1990; Werner & Anholt, 1993). We suggest that competition coupled with late seasonal energetic demands would cause female deer to increase movement, as these individuals would need to acquire resources to build reserves for winter and ovulation (Bender & Hoenes, 2017; Bowyer, 1991). In a system with limited exploitative competition, the role of interference competition on individual speed is not as well examined, and the mechanisms driving this behavior in white-tailed deer should be further investigated. We postulate that deer may be limiting speed to reduce potential encounters with cattle or deer may be reducing exploratory movements focusing on core habitats that meet their immediate needs.

White-tailed deer experienced a shift in their realized niche as a function of cattle competition, suggesting competition resulted in niche partitioning (Finke & Snyder, 2008; Leo et al., 2015; Loft et al., 1991; Petroelje et al., 2021; Prins, 2000). We expected white-tailed deer to increase their use of areas with greater woody cover, as these areas can serve as a refuge from cattle (Cooper et al., 2008; Fulbright & Ortega-S, 2013; Owens et al., 1991). Additionally, as browsers, deer might have made greater use of woody cover as potential forage source as vegetation in region would be entering winter senescence (Esmaeili et al., 2021; Fulbright & Ortega-S, 2013). Our results also suggest cattle displaced white-tailed deer from sites of better quality habitat, as deer selection for sandier soils increased with cattle stocking density. Sandier soils are often associated with poorer quality habitat for white-tailed deer (Foley et al., 2018), which may affect deer nutrition and survival and increased use of these poorer quality sites could have demographic consequences (Ayotte et al., 2020; Oates et al., 2021). Alternatively, it is possible, this increased selection for sandier sites could be evidence of facilitation as cattle grazing can stimulate forb growth on sites with exceedingly sandy soils (Fulbright et al., 2021). However, we do not suspect this to be the case because rainfall was minimal during our study which likely would have limited autumn forb production (Fulbright et al., 1990).

White-tailed deer space use was not influenced by the distribution of water or roads, indicating these features may be either inconsequential for white-tailed deer space use during our study or cattle were unable to restrict access to the features. The lack of response of white-tailed deer selection to water sources could have been driven by the season in which our study occurred, as our study occurred during the cooler part of the year when individual water needs would have been reduced. Alternatively, water may have been such a significant resource that deer were unable to alter their use of it and instead altered the timing of water use to avoid cattle. Cooper et al. (2008) observed comparable results when cattle grazing did not influence white-tailed deer distribution in relation to roads, but they did document that deer were closer to water sources than expected at random. However, Cooper et al. (2008) noted that a drought developed during the warm season of their study, possibly explaining this effect.

Opportunities to isolate the mechanisms of competition are rare in nature and require experimental approaches (Hsu et al., 1981; Ping et al., 2011; Smallegange et al., 2006). Previous studies limited exploitative competition by replacing resources as they were consumed; however, we demonstrated that exploitative competition can be minimal when studies focus on the immediate effects of experimentally instigated interactions (Ping et al., 2011; Smallegange et al., 2006). Our approach allowed us to eliminate potential biases associated with replacing resources, as it is rare for these resources to be distributed homogenously, which can congregate competitors and intensify competitive interactions. Furthermore, we stocked cattle across a wide gradient of densities from low to nearly twice what is considered high for the region (high-moderate grazing density for region: 8–5 AU/km^2; Montalvo et al., 2020), which allowed us to demonstrate how competitive effects of the dominant competitors' density influenced the subordinates' behavior. Previous research examined the competitive effects of cattle competition on deer at a few designated densities (Cooper et al., 2008; Depew, 2005; Ortega et al., 1997). We were unable to capture the long-term temporal aspects of exploitative and interference competition, in which we expect seasonal variation in resources and habituation to competitors may alter animal behavior and space use. Future studies should examine the duration and intensity in which exploitative competition develops and its influences on the distribution of wildlife. Human presence could have confounded our results and influenced deer behavior. However, human density on our site was extremely low and standardized across treatments. Ranch personnel visited all pastures to maintain water sources whether cattle were present or not, and fear of humans by deer should be minimal since hunting was prohibited on the property. Therefore, we suspect human influences on our results should be minimal.

Our results suggest livestock can impact wildlife behavior even at the conservative stocking densities and further illuminates how competition drives animal ecology and species interactions. Competition with livestock can potentially impact wildlife fitness, reducing nutritional condition and subsequently impacting adult survival and offspring recruitment (Ayotte et al., 2020; Jenks & Leslie, 2003; Piasecke & Bender, 2009). We further demonstrated how niche partitioning processes may be impacted by interference competition before the effects of exploitative competition, revealing that the development of these mechanisms may occur at different temporal scales. By understanding these mechanisms and their influences on niche space, we can evaluate species responses to competitors and employ management strategies to alter the intensity and outcome of the competitive interactions. These deeper understandings of the competitive process will become increasingly important as global demands drive land conversions to agriculture, and the coexistence of livestock and wildlife and integration of multiple landscape objectives become a greater priority on new and existing working landscapes for economic and conservation concerns.

AUTHOR CONTRIBUTIONS

Bryan D. Spencer and Michael J. Cherry designed the study. All authors contributed to data collection and funding procurement. Bryan D. Spencer conducted all analyses and wrote the first draft. All authors contributed to manuscript revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and statistical code (Spencer, 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.10839820.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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