CATTLE, DEER, AND NILGAI INTERACTIONS

A Dissertation

by

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Submitted to the College of Graduate Studies
Texas A&M University–Kingsville
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2016

Major Subject: Wildlife Science

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ABSTRACT

Cattle, Deer, and Nilgai Interactions

(August 2016)

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Co-Chairmen of Advisory Committee: Dr. Timothy E. Fulbright and Dr. J. Alfonso Ortega-S.

Consensus regarding large ungulates impacts, on one another and vegetation, is lacking. My objectives were to: 1) evaluate literature regarding cattle (*Bos* species) and deer (*Odocoileus* species) research across North America; 2) determine if cattle grazing grasses increases forbs preferred by white-tailed deer (*Odocoileus virginianus*); 3) determine the importance of abiotic and biotic variables on plant species richness; and 4) determine if diet composition of white-tailed deer, nilgai (*Boselaphus tragocamelus*), and cattle follows the body size and rumino-reticulum to body weight ratio hypotheses.

I quantitatively evaluated 85 publications reporting cattle grazing effects on deer and habitat variables important to deer (e.g., objective 1). Across North America: 1) forbs had a higher probability of increasing in cattle grazed areas in more mesic ecoregions; 2) cattle in forested ecoregions have a higher probability of adversely affecting deer because cattle activities reduced potential woody cover and browse and increased probability of altering deer space use; and 3) cattle-deer diet overlap increased with increasing cattle stocking rate and during seasons in which grasses were dormant.

To evaluate large ungulate impacts on vegetation, I sampled standing crop of herbaceous vegetation and species richness during peak growing seasons at 300 randomly allocated paired (grazed and non-grazed) sampling locations on 4 East Foundation ranches across South Texas, 2012–2015 (e.g., objectives 2–3). Grass utilization by cattle resulted in greater standing crop of forbs preferred by white-tailed deer relative to the non-grazed area, but the increased forb standing crop was biologically insignificant (e.g., $<1 \text{ kg} \cdot \text{ha}^{-1}$). Forb standing crop across South Texas is not biologically affected by cattle utilization of grasses. However, grazing by large herbivores (cattle, deer, and nilgai), along with site productivity and environmental factors, are all important components influencing vegetation species richness across South Texas.

I seasonally collected cattle, deer, and nilgai fecal samples across six 2 500 ha study sites located on 4 East Foundation ranches, 2012–2015 (e.g., objective 4). I investigated large ungulate diets by analyzing the carbon and nitrogen stable isotope signature of fecal samples. Results largely agreed with classification of deer as browsers and cattle as grazers. However, Nilgai food habits were generally more similar to browsers.

Cattle, deer, and nilgai are compatible on rangelands with the implementation of conservative management practices. The principal management factor to maintain large ungulate compatibility on rangelands is to balance animal stocking rates with available resources important to large ungulates.

ACKNOWLEDGMENTS

First, I would like to thank my co-advisors, T. Fulbright and J.A. Ortega-S., and my committee members, D. Hewitt and T. Boutton, for sharing their knowledge and experiences with me throughout the past four years. I would like to thank the East Foundation, major funding source, the Meadows Professorship in Semiarid Land Ecology, and the Caesar Kleberg Wildlife Research Institute (CKWRI) and Texas A&M University–Kingsville. In addition I am grateful to D. Wester and S. Webb for their statistical advice and assistance; R. Obregon and South Texas Natives for their assistance in designing and building our mobile drying room; A. Hyodo for isotopic analyses of plant and animal tissues in the Stable Isotopes for Biosphere Sciences Lab at Texas A&M University in College Station; E. Grahmann and J. Folks for assistance with list of non-preferred deer forbs; S. Goertz, E. Grahmann, and F. Smith for assistance in identifying unknown plants; K. Allred, D. Belleny, K. Brewster, L. Briones, A. Canul, K. Castro, D. Drabek, N. Edmund, F. Elias, W. Frederick, H. Hernandez, A. Jackson, L. Koczur, C. Lange, D. McBee, B. Mitchell, B. Newman, T. Reagan, R. Saenz, A. Ortega-S. Jr., and S. Young for their assistance with field and lab research; Houston Safari Club Dan L. Duncan Scholarship, Promoting Postbaccalaureate Opportunities for Hispanic Americans Scholarship, South Texas Quail Coalition Scholarship, Phil Plant Scholarship, Rebecca Palmer Graduate Student Scholarship, and Rene Barrientos Tuition Assistance for contributing funding.

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CHAPTER I

A REVIEW OF NORTH AMERICAN CATTLE-DEER COMPATIBILITY

Introduction

Livestock grazing is the dominate land use on rangelands which comprise 30–40% of terrestrial area globally (Briske et al., 2015). Rangelands are also important habitat for wildlife; for example, the majority (84%) of mammal species in the United States spend at least part of their time on rangelands (Hart, 1994). Consequently, livestock impacts to wildlife have become one of the most controversial natural resource issues in the western US (Holechek, 1991). Two strikingly different points of view regarding livestock and wildlife exist in the literature. One point of view is that livestock grazing negatively impacts wildlife habitat and ecosystem function and complete removal of livestock is needed so the ecosystem can recover (Belsky et al., 1999; Fleischner, 1994). The opposing point of view is that cattle grazing, with proper implementation, can be used as a wildlife habitat management tool and that grazing by cattle and wildlife are compatible land uses (Holechek, 1991; Krausman et al., 2009; Leopold, 1933).

Most reviews of livestock effects on wildlife have been qualitative (Belsky and Blumenthal, 1997; Fleischner, 1994; Krausman et al., 2009), concentrated on western US (Belsky and Blumenthal, 1997; Fleischner, 1994; Jones, 2000) with little inclusion of studies conducted in other regions (Belsky et al., 1999; Krausman et al., 2009), and have focused on small and often geographically constrained species, ranging from aquatic species to small mammals (Fleischner, 1994; Jones, 2000). Qualitative reviews may be biased (Jones, 2000) because they are a subjective summarization of narrative data. Conversely, quantitative reviews extract data for statistical analysis, thus objectively evaluate impacts, and thereby reduce biases associated with qualitative reviews.

Rangeland Ecology and Management

I selected interaction between cattle (*Bos* species) and deer (*Odocoileus* species) for this review because: 1) cattle are the most numerous form of livestock in North America (Belsky et al., 1999) providing revenue for millions of humans (Sayre et al., 2013); 2) deer are the most economically important native wildlife species on North American rangelands for wildlife recreation (Curtis, 2002; Watkins et al., 2007); 3) more research has been completed on deer and cattle than most other species, thus these species provide a greater database for drawing conclusions; and 4) a comprehensive review of cattle-deer interactions is nonexistent in scientific literature. My objective was to determine the response of deer and habitat variables important to deer to grazing by cattle on lands across North America. I quantitatively evaluated publications reporting: 1) influence of cattle grazing on forb availability because forbs are an important constituent in deer diets (Fulbright and Ortega-S., 2013; Krausman et al., 1997); 2) woody plant responses to cattle grazing because woody plants are an important source of cover and food (e.g., browse and mast) for deer (Fulbright and Ortega-S., 2013; Krausman et al., 1997); 3) cattle effects on deer use of space; and 4) diet overlap among cattle and deer because increasing space use (i.e., home range size) and increasing diet-overlap may result from or indicate potential competition between the species (Garrott et al., 1987; Stewart et al., 2011).

Methods

I reviewed 2 685 publications on cattle-deer interactions in North America and extracted data, included in ≥1 data set(s), from 85 publications (Fig. 1.1; Appendix A) that met the following criteria: 1) cattle were the only livestock species; 2) there was no disturbance (e.g., fire or human-induced alteration to vegetation community) within 2 years of data collection; and 3) research was conducted on non-cultivated lands (i.e., cultivated lands included food crop or fescue pasture).

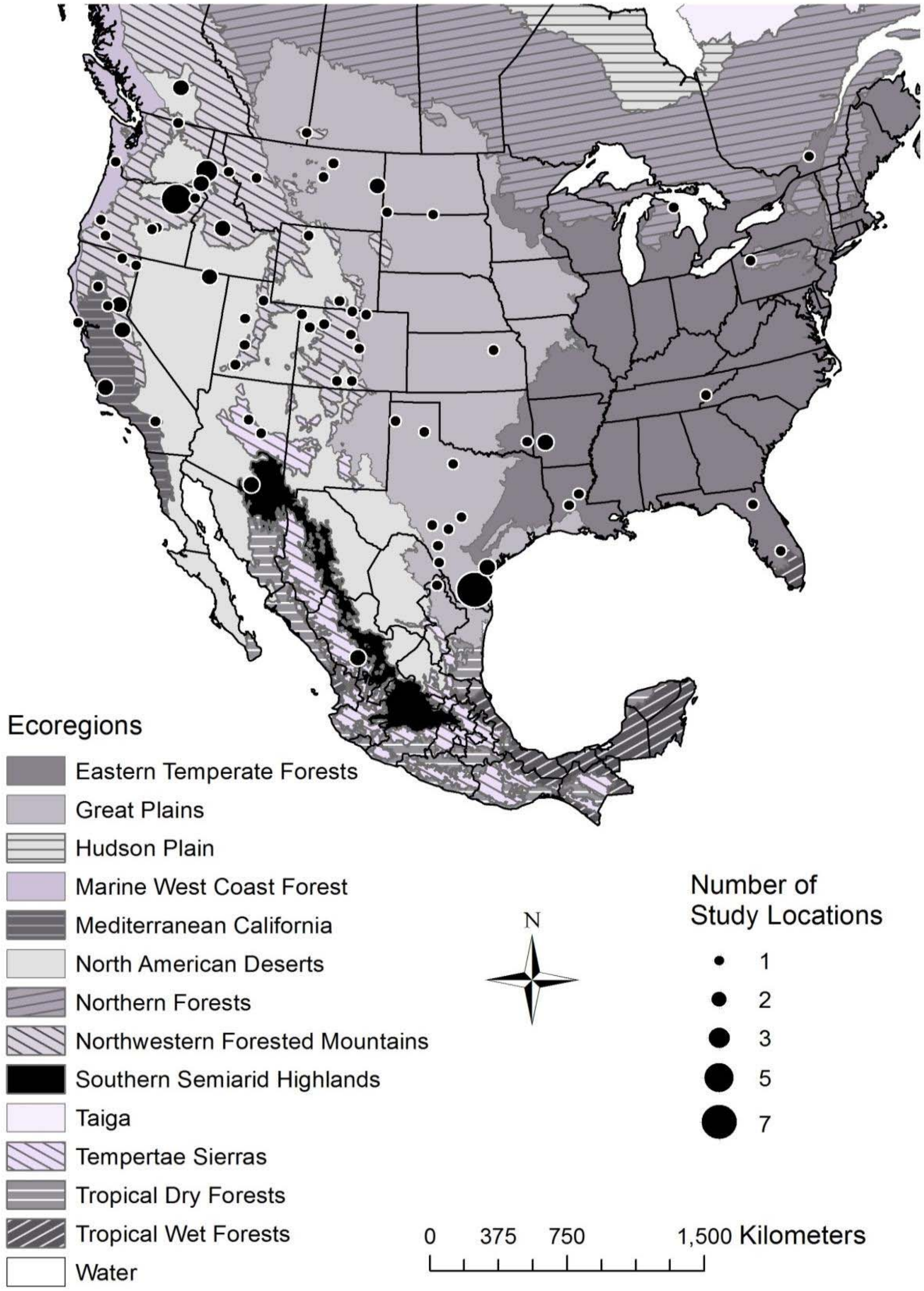

Figure 1.1. Locations of 85 studies conducted across North America ecoregions on interactions between cattle and deer, 1929–2014. Research spanned 85 years and may have been conducted at same location for >1 publication or >1 location for one publication.

Vegetation communities influence cattle-deer interactions and vary spatially and temporally (Bork and Werner, 1999), thus spatially and temporally distinct observations (hereafter: observations) extracted from publications were not considered repeated measures. Multiple methods (e.g., cover, density, frequency, species richness, or standing crop) were employed across publications to examine vegetation response (forbs, grasses, woody plants), thus vegetation response was recorded as a trinomial variable that included decreased, not affected, or increased in cattle grazed compared to non-grazed areas. In addition, I extracted data on animal stocking rates, annual rainfall, dominant soil texture, season, and geographic location because they influence vegetation communities. When characteristic data were not included in the publication, I contacted multiple sources (including but not limited to, authors, federal and state government agencies, and other publications) to obtain information to include in my statistical analyses.

I conducted the statistical analyses using SAS (version 9.3, SAS Institute, Cary, NC, USA). For data sets with a categorical dependent variable (vegetation and space use data sets), I first analyzed responses of observations using contingency table chi-square test. Then, for each data set, I determined the model that best described the relationship of the observations with explanatory variables; I began with a full model and removed variables from each model when $P > 0.10$ (Peterman, 1990).

Each full model was blocked by season and soil texture, included animal stocking rate (cattle and/or deer) and annual rainfall as continuous explanatory variables, and geographic location (latitude and longitude) of study location as covariates. Including geographic location as a covariate accounted for vast spatial distribution, study locations with multiple observations (e.g., if reported data from multiple sites, seasons, and/or years), and spatial gradient of deer species across North America. To avoid over-fitting each model and biasing variances of parameter estimates, collinear predictors (condition index of model > 30) were not included in the model (Haque et al., 2002). Annual rainfall was a collinear predictor with geographic location, thus not included in any model. When latitude and longitude were collinear predictors, a single geographic location parameter (calculated as latitude × longitude) was included as a covariate in the model.

Forbs

I included 351 observations from 24 publications where researchers concomitantly reported response of grasses and forbs to grazing by cattle compared to non-grazed areas. Forb response (nominal distribution) was modeled with a multinomial logistic regression using Proc Logistic (generalized logit link function); the full model also included grass response as an explanatory variable. Forb response was not modeled as ordinal distribution, due to failing assumptions for both full and partial proportional odds model.

Woody plants

I included 161 observations from 26 publications when researchers reported response of woody plants to grazing by cattle compared to non-grazed areas. Woody plant response (ordinal distribution) was modeled with a proportional odds model using Proc Logistic (cumulative logit link function).

Use of space

I included 69 observations from 32 publications when researchers comparatively reported deer use of space when cattle were and were not present. Data were entered as binary response: 1) “no” indicated cattle had no effect on deer use of space and included observations when deer only maintained distance from cattle, but did not otherwise change their use of space; and 2) “yes” indicated deer utilized alternative vegetation communities (not used when cattle were absent) or increased home range size when cattle were present. Deer shift in use of space was modeled with a binary logistic regression using Proc Logistic (logit link function).

Diet overlap

I included 118 observations from 26 publications when researchers reported percent diet overlap among cattle and deer or reported dietary intake metric of vegetation species so I could calculate percent diet overlap. Multiple methods were employed in the publications to observe diets of species (i.e., bite counts, microhistological, rumen content analysis) and to calculate percent diet overlap (i.e., Kulcyznski's Similarity Index, Morista-Horn Index, Pianka Index); these are biases associated with this analysis I could not account for. Percent diet overlap was modeled with a general linear model using Proc GLM. Because percent diet overlap is bound between 0–1, residuals were tested to corroborate general linear model assumptions; in addition, results were verified with a generalized linear mixed model with a beta distribution (logit link function) using Proc Glimmix (Dickey, 2010).

Results

Forbs

The primary rationale for cattle-deer compatibility, specifically employing cattle grazing as a wildlife management tool, originates from the theory that cattle grazing decreases grasses, thereby making grasses less competitive with forbs in climax grasslands (e.g., dominated by grasses with few forbs present), resulting in an increase in forbs (Leopold 1933; Vavra 2005). The majority of observations (51%) were from study sites in western North America, followed by central (33%), then eastern (16%) North America. In cattle grazed compared to non-grazed areas, grasses decreased in 66% of observations across North America, of which forbs concomitantly increased in 15% of observations (Table 1.1). Forb response (decreased, not affected, or increased) was not related ($P \geq 0.514$) to grass response or cattle stocking rate (e.g., biotic factors). Not accounting for grass response, observations of forb response equally (one-third of observations) decreased, were not affected, or increased in cattle grazed compared to non-grazed areas ($P = 0.132$). While not related to biotic factors, the probability forbs would display a response (whether decreased or increased versus were not affected) was related ($P \leq 0.038$) to abiotic factors (soil texture and geographic location). Although, the probability forbs decreased or forbs increased had similar relationships with abiotic factors (Fig. 1.2). Forbs are 46% and 52% more likely to respond (decreased and increased, respectively) than show no response on clay compared to loam textured soils ($P \leq 0.026$). When accounting for the relationship with geographic location, however, the probability forbs increased or decreased in response to cattle grazing is similar among clay and loam textured soils (Fig. 1.2). With northward progression across North America (each additional decimal degree increase in latitude), there is a 21% and 12% increase in the odds that forbs will respond (decrease and increase, respectively; $P \leq 0.002$). With eastward progression across North America (each additional decimal degree increase in longitude; i.e., $-120 + 1 = -119$), there is a 5% and 10% increase in the odds forbs will respond (decrease and increase, respectively; $P < 0.001$). In northern and eastern North American ecoregions (more mesic ecoregions), forbs have a higher probability of displaying a response (e.g., increase in the odds with northward and eastward progression across North America), whether the response is to increase or decrease, compared to having no response in cattle grazed compared to non-grazed areas (Fig. 1.2).

Table 1.1. Frequency of observations (*n* = 351) by research method reported in 24 publications from research in North America to concomitantly examine response of grasses and forbs in cattle grazed compared to non-grazed areas, 1929–2014.

Response of grasses	Response of Forbs		
Grasses decreased	Frequency of observations (%)		
Method	Decreased	No effect	Increased
[1]Cover	3	11	5
[2]Density	1	2	1
[3]Frequency	—	—	—
[4]Species richness	—	—	—
[5]Standing crop	20	14	9
No effect on grasses	Frequency of observations (%)		
Method	Decreased	No effect	Increased
Cover	—	1	1
Density	—	—	—
Frequency	—	—	—
Species richness	—	—	—
Standing crop	1	2	—
Grasses increased	Frequency of observations (%)		
Method	Decreased	No effect	Increased
Cover	4	5	2
Density	—	—	—
Frequency	3	1	10
Species richness	—	—	1
Standing crop	1	1	1

[1] Cover included methods that recorded area of vegetation coverage (percent or cm) and green vegetation index (leaf surface area coverage).

[2] Density is defined as number of plants per area.

[3] Frequency is defined as proportion of plots species is present.

[4] Species richness is defined as number of species per area.

[5] Standing crop is defined as biomass (or weight) of plants per area.

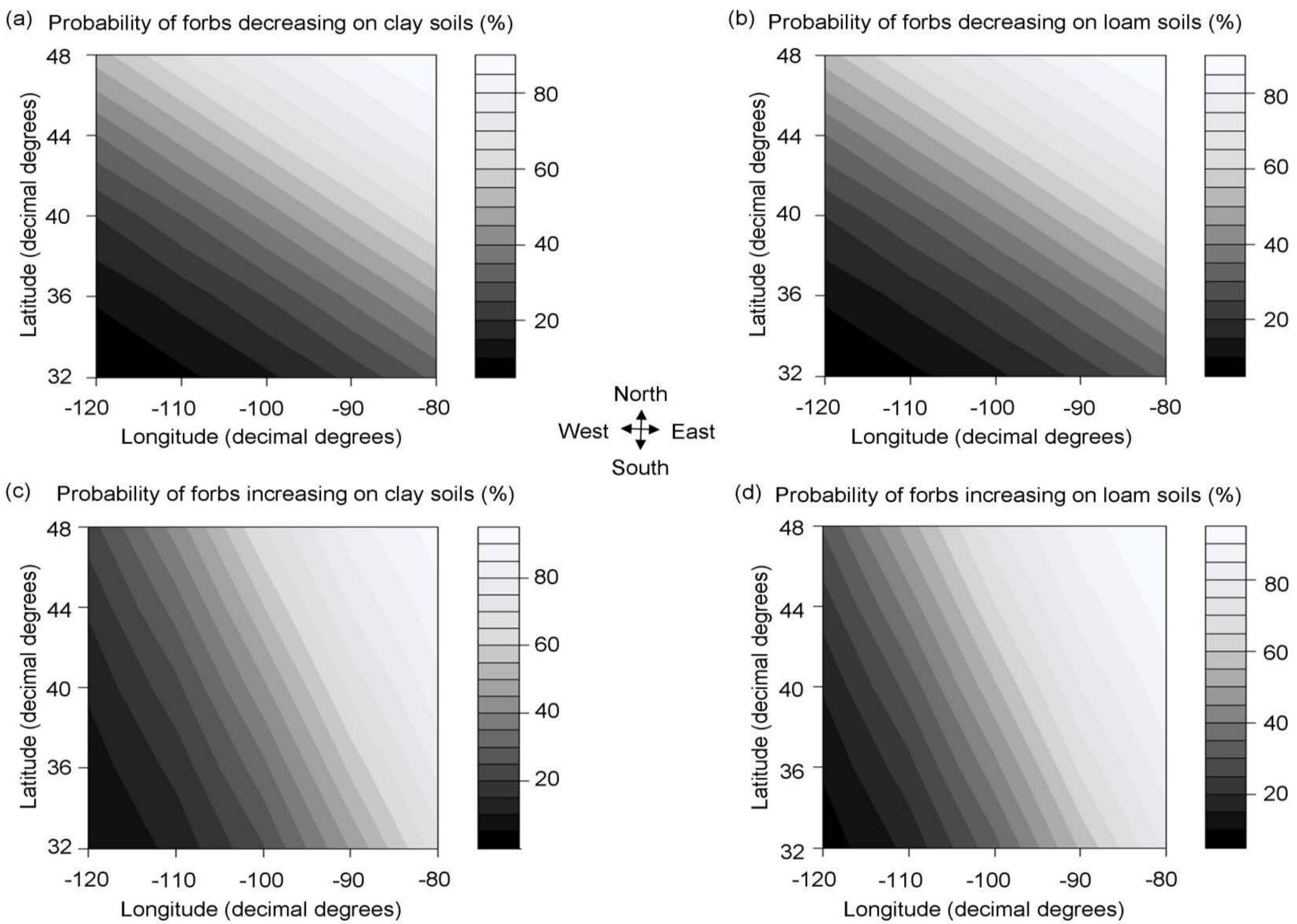

Figure 1.2. Probability forbs decreased (a,b) or increased (c,d) versus were not affected in cattle grazed compared to non-grazed areas as it related to soil texture [clay (a,c) or loam (b,d)] and geographic location across North America; reported in 24 publications, 1929–2014.

Woody plants

Woody plants within the useable space of deer provide deer with potential: 1) hiding cover from predators; 2) cover to alleviate extreme weather conditions; and 3) primary, year-round deer food reserve (Fulbright and Ortega-S., 2013; Krausman et al., 1997). Responses of woody plants within the useable space of deer were quantified in publications as changes in factors that could affect potential woody cover and/or food for deer (hereafter: woody plants): 1) canopy or stem cover (area or percent cover); 2) density; 3) frequency; and 4) standing crop of browse. The majority of observations (78%) were from study sites in western North America. In areas grazed by cattle compared to non-grazed areas, woody plants decreased in 49% of observations, were not affected in 37% of observations, and increased in 14% of observations ($P < 0.001$; Table 1.2). The response of woody plants were related ($P \leq 0.042$) to geographic location (abiotic factor) and cattle stocking rate (biotic factor; Fig. 1.3). With eastward progression across North America (each additional decimal degree increase in longitude; i.e., -120 + 1 = -119), there is a 2% increase in the odds woody plants will decrease in areas grazed by cattle ($P = 0.042$). At first, the relationship of woody plant response and cattle stocking rate determined from my model appeared counter-intuitive; there is a 28% reduction in the odds of woody plants decreasing (P $=0.026$) in response to grazing for every 0.1 AUY (animal unit year) ha^{-1} increase in cattle stocking rate (i.e., increase cattle stocking rate from 1 AUY per 10 ha to 1 AUY per 5 ha). Further examination of the data revealed: 1) woody plants decreased in eastern forested ecoregions, which had lower cattle stocking rates compared to western grassland and desert ecoregions; and 2) woody plants increased in western grassland and desert ecoregions, which had higher cattle stocking rates compared to eastern forested ecoregions. Thus, this model captured cattle stocking rate differences across North America. In eastern forested ecoregions where cattle

Table 1.2. Frequency of observations (*n* = 161) by research method reported in 26 publications from research in North America to examine response of woody plants within the useable space of deer, which provide deer with potential woody cover and/or food, in cattle grazed compared to non-grazed areas, 1929–2009.

	Frequency of observations (%)		
Method	Decreased	Not affected	Increased
[1]Cover[1]	25	18	5
[2]Density	4	2	—
[3]Frequency	5	8	4
[4]Species richness	—	—	—
[5]Standing crop	15	9	5

[1] Cover included methods that recorded area of canopy coverage (percent or cm) and area of stem coverage (stems of woody plants and stem volume of woody plants).

[2] Density is defined as number of plants per area.

[3] Frequency is defined as proportion of plots species is present.

[4] Species richness is defined as number of species per area.

[5] Standing crop is defined as biomass (or weight) of plants per area.

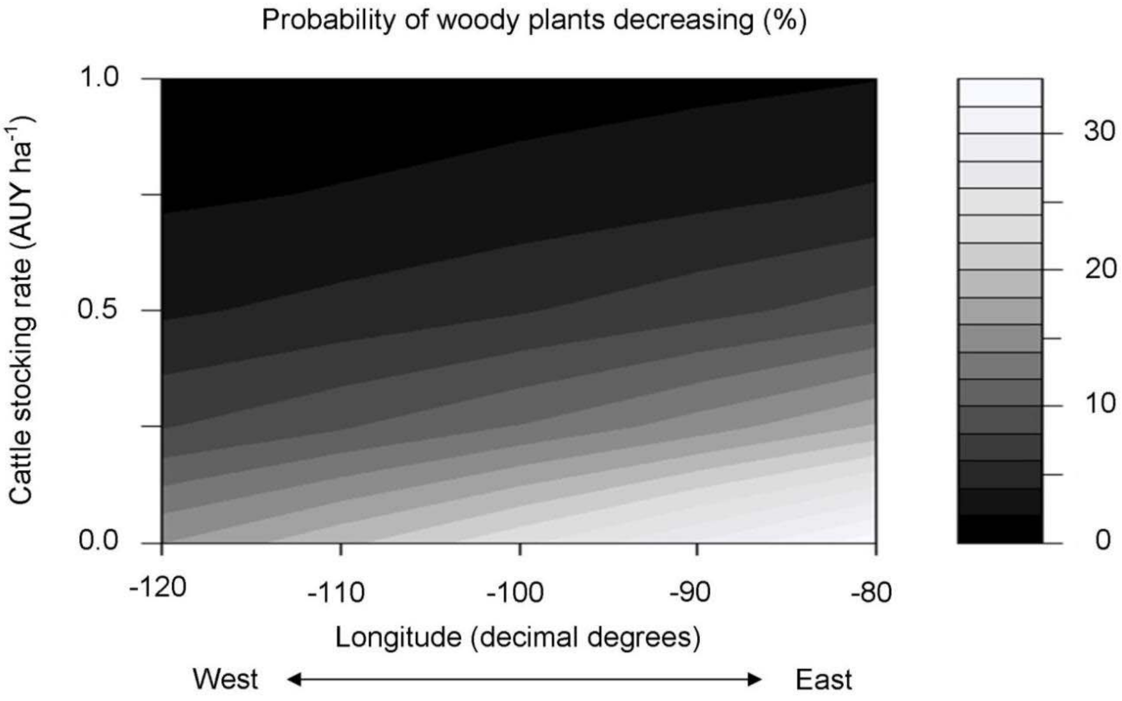

Figure 1.3. Probability that woody plants within the useable space of deer, provides deer with potential woody cover and/or food, decreased versus were not affected or increased in areas where cattle grazed compared to non-grazed areas across North America as it related to cattle stocking rate [animal unit year (AUY) ha^{-1}] and longitude (west to east across North America); reported in 26 publications, 1929–2009. Cattle stocking rate was lower in western North America compared to eastern North America, thus woody plants in cattle grazed versus non-grazed areas have a higher probability of decreasing in eastern North America under lower cattle stocking rates compared to western North America.

graze compared to non-grazed areas, there is a higher probability that woody plants will decrease compared to western grassland and desert ecoregions, under lower cattle stocking rates compared to western ecoregions.

Use of space

Deer select habitat to meet their basic needs for survival while minimizing energy expended (Brown, 1992; Hygnstrom and VerCauteren, 2000). Smaller deer home range sizes are typically observed in habitats with abundant forage and reduced competition (Garrott et al., 1987; Stewart et al., 2011). The majority of observations (55%) were from study sites in western North America, followed by central (39%), then eastern (6%) North America. In two-thirds of observations ($P = 0.022$), deer utilized alternative vegetation communities that were not used if cattle were absent or deer had larger home range sizes when cattle were present (hereafter: shift in space use). When cattle were present compared to when cattle were absent, deer selected vegetation communities with less herbaceous forage, that were on steeper slopes, and that had not been grazed by cattle. The models of the relationship of shift in space use and predictor variables either indicated a lack of fit, over dispersion, or collinearity of predictor variables. This was probably due to the small sample size of this data set ($n = 69$ observations) and variability across North America. While I do not have confidence in the precision of the estimates, the analysis revealed prospective associations. These prospective associations included that deer have a higher probability of shifting space use as cattle stocking rate increases. Also, the probability of a shift in space use is related to geographic location. Across observations, deer had the highest probability (39% yes compared to 14% no; $n = 36$) of shifting use of space in forested ecoregions (i.e., Eastern Temperate Forest, Northwestern Forested Mountains, Temperate Sierras). While deer were just as likely to shift space use as not in non-forested, open ecoregions (i.e., Great Plains, North American Deserts; 21% yes compared to 19% no; $n = 28$) and mixed forested/open ecoregions (i.e., Mediterranean California, Southern Semiarid Highlands; 4% yes compared to 3% no; $n = 5$). In more open ecosystems when cattle were present, deer were just as likely to shift space use as not. Conversely, in forested ecosystems when cattle were present, deer more likely used alternative vegetation communities, with less herbaceous forage or vegetation communities on steeper slopes, and deer had larger home ranges.

Diet overlap

Cattle consume 5× more forage daily than deer consume; thus at 20% diet overlap, one cattle AUY (mother cow-calf pair) consumes the daily equivalent of forage of one deer. Observations were fairly equally dispersed across North America; 28% from western, 37% from central, and 35% from eastern North American study sites. Accounting for geographic location (covariates in model), cattle stocking rate and season explained almost half (47%) of the variation in predicted cattle-deer diet overlap. Diet overlap among cattle and deer increased 5% ($P < 0.001$) for every 0.1 AUY ha^{-1} increase in cattle stocking rate (i.e., increase cattle stocking rate from 1 AUY per 10 ha to 1 AUY per 5 ha), but diet overlap was not related to deer density ($P = 0.544$). In addition, diet overlap was 12–14% greater ($P < 0.001$) during winter and spring compared to autumn or summer. Diet overlap was >20% during winter and spring seasons, regardless of cattle stocking rate, and reached 20% during autumn and summer when cattle stocking rate was 0.17 AUY ha^{-1} (e.g., 1 AUY per 5.9 ha; Fig. 1.4). When forage is limiting and diet overlap >20%, competition for forages among cattle and deer is possible. Typically, cattle select for grasses (Armstrong, 1981; Gallina, 1993; Mackie, 1970). However, when potentially less grass was available, due to higher cattle stocking rate and during non-peak grass growing seasons, cattle switched to forages consumed by deer. The availability of grasses, not deer density, determined

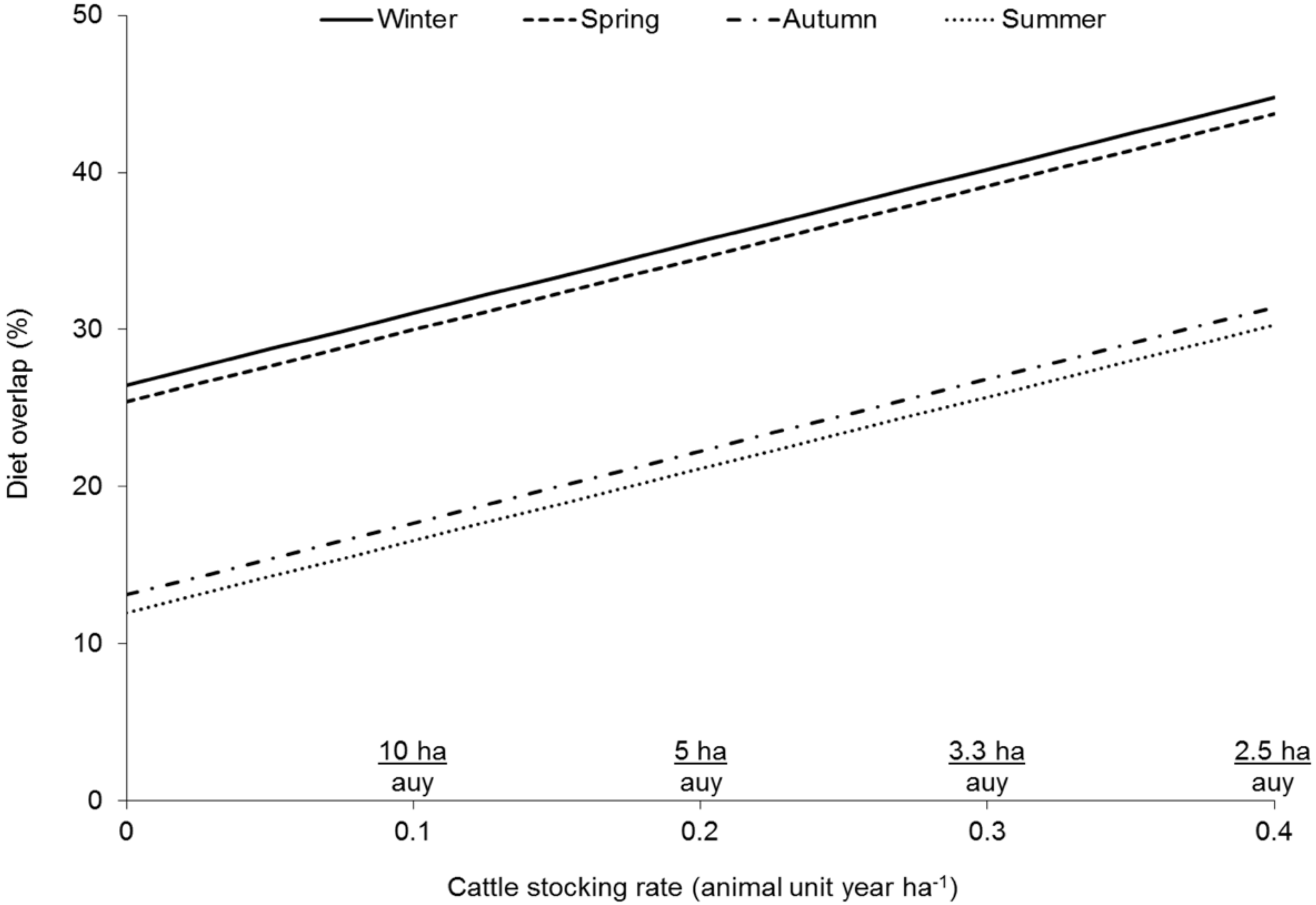

Figure 1.4. Seasonal diet overlap (%) among cattle and deer in North America as it relates to cattle stocking rate expressed as animal unit year ha^{-1}; reported in 26 publications, 1947–2001.

when cattle and deer diets overlapped.

Discussion

Ecoregions, vegetation communities, environmental variables, and even species of deer (*Odocoileus* species) differ across North America. Yet with this quantitative analysis, I discovered noteworthy relationships governing cattle-deer compatibility on lands across North America. These relationships include: 1) forbs have a higher probability of responding to cattle grazing (increased or decreased versus were not affected) in more mesic ecoregions; 2) cattle in forested ecoregions have a higher probability of adversely affecting deer; and 3) cattle consumed the same forages as deer when grass availability was potentially lower because of increasing cattle stocking rates and during non-peak grass growing seasons.

Forbs were less likely to be affected in areas where cattle grazed compared to non-grazed areas in western North America. The weaker than expected influence of cattle grazing affecting vegetation was likely because western North American ecosystems are drier and precipitation is more variable (Von Wehreden et al., 2012). The idea that grazing of grasses by cattle makes grasses less competitive with forbs, allowing forbs to increase is based on traditional Clementsian (1916) succession theory where succession is directional and climax communities are in equilibrium with biotic and abiotic factors (Kayes et al., 2010). In western North America (arid and semiarid ecoregions), however, vegetation succession may not be directional and may not develop toward an equilibrium state. Vegetation dynamics in arid and semiarid portions of western North America may operate under non-equilibrium dynamics (Von Wehrden et al., 2012), where abiotic factors control vegetation dynamics more strongly than biotic factors (Ellis and Swift, 1988). Applying cattle grazing as a management tool to increase forbs for deer has a higher probability of success in more mesic ecoregions of eastern North America where succession is often directional and vegetation dynamics are more strongly influenced by biotic factors. However, more research is needed to determine under what conditions forbs would increase in cattle grazed areas; because based on the little research conducted in eastern North America, forbs were just as likely to decrease, as increase, in cattle grazed areas.

Cattle in forested ecoregions had the highest probability of negatively affecting deer habitat because grazing by cattle reduced potential woody cover and browse and increased probability of altering deer space use compared to more open ecoregions. In forested ecosystems, understory vegetation can provide deer with food and cover, but it is typically less abundant because sunlight is reduced to vegetation under a forest canopy (Massé and Côté, 2009). Disturbance to understory vegetation in forested ecoregions adversely affects deer use of space (Lashley et al., 2015). Thus, in forested ecosystems where vegetation important to deer is already limiting, disturbance to vegetation by cattle grazing adversely affected deer.

There is a lot of natural variability, such as climatic influences in different ecosystems, different vegetation communities, variety of plant species and their interactions with one another, affecting forages available to cattle and deer across North America. Yet cattle stocking rate and season of the year, which influenced the availability of grasses, explained almost half of the variation in cattle-deer diet overlap across North America. Deer are not switching to forages (grasses) cattle select since deer stocking rate did not influence cattle-deer diet overlap. Instead when grasses are limited, cattle are switching to forages deer select (e.g., forbs and woody browse plants).

This quantitative analysis of the past 85 years of published literature indicates that cattle and deer are compatible on North American lands with the implementation of conservative cattle grazing management practices. The principal management factor to maintain cattle-deer compatibility on North American lands is adjusting cattle stocking rate to sustain vegetation important to both cattle and deer by balancing utilization with vegetation recovery.

CHAPTER II

DOES CATTLE GRAZING INCREASE FORBS PREFERRED BY WHITE-TAILED DEER IN SOUTH TEXAS?

Introduction

Aldo Leopold (1933) suggested in his book *Game Management* that cattle (*Bos* spp.) grazing could be used as a wildlife habitat management tool. Leopold's idea was based on the premise that cattle mainly consume graminiods (Armstrong, 1981; Gallina, 1983; Mackie, 1970), and that reduction in graminoids provides forbs a competitive advantage which allows standing crop of forbs to increase (Vavra, 2005). Thus, wildlife that utilize forbs should benefit from moderate cattle grazing (Kie and Loft, 1990). Since Leopold's time, applied ecologists have used cattle as a habitat management tool for a variety of wildlife species, from songbirds to ungulates (i.e., Anderson and Scherzinger, 1975; Sliwinski and Koper, 2015; Thill and Martin, 1989). In addition, extension and popular literature (i.e., Ellis, 2014; Lyons and Wright, 2003) have promoted the use of cattle grazing to increase forbs for white-tailed deer (*Odocoileus virginianus*). An increase in forbs would benefit white-tailed deer because when available, forbs comprise a larger proportion of deer diets than other forage classes (Arnold and Drawe, 1979; Drawe and Box, 1968). However, although this idea has been suggested, there is no empirical evidence cattle grazing increases forbs preferred by white-tailed deer (Fulbright and Ortega-S., 2013).

Reported effects of cattle grazing on forbs are inconsistent in the literature, and it is unclear if grazing is a useful tool to increase forbs. In mesic grasslands, cattle grazing increased forbs (Hayes and Holl, 2003; Jenks et al., 1996; Thill and Martin, 1989, 1986; Towne et al., 2005). However, in semiarid and arid environments, some researchers concluded cattle grazing had no impact on forbs (Jones, 2000; Ortega et al., 1997) while other researchers concluded cattle grazing increased forbs (Evans, 1986; Holechek, 1991; Ruthven, 2007). In mesic environments, forage responses to cattle grazing may be more predictable (Bleich et al., 2005), but not in drier, more stochastic environments (Fulbright and Ortega-S., 2013).

Consensus may be lacking in published literature because responses of forages to cattle grazing are confounded across gradients of precipitation, soil series, plant communities, and seral stage of succession (Fulbright et al., 2008; Georgiadis et al., 1989; Krausman et al., 2009; Vavra, 2005). In addition, there is a paucity of studies that employed experimental designs to account for the natural spatial variability of vegetation communities (Bork and Werner, 1999) and patchiness of cattle grazing across the landscape (Andrew, 1988; Landsberg et al., 2003, 1999; Pringle and Landsberg, 2004). Furthermore, few studies directly measured the standing crop of forbs (Fulbright and Ortega-S., 2013), and instead drew inferences from other metrics, such as dietary intake of forbs by deer.

My objective was to determine if cattle utilization of grasses increased forbs preferred by white-tailed deer by comparing standing crop of forages in non-grazed grazing exclosures to paired grazed areas at the landscape scale. In climax grasslands, the reduction of grass by cattle grazing gives forbs a competitive advantage, thus standing crop of forbs should increase under light to moderate cattle grazing (Holechek et al., 2011). Under heavy cattle grazing, when grasses become limited, cattle will consume available forages thereby reducing the standing crop of forbs (Ellis, 2014; Holechek et al., 2011; Lyons and Wright, 2003). I hypothesized standing crop of forbs would increase with increasing cattle grass utilization, with forbs preferred by deer increasing up to some moderate level of grass utilization and forbs not preferred by deer increasing above a moderate level of utilization, and then declining with increasing utilization (Fig. 2.1).

Methods

Study site description

I selected six 2 500 ha study sites (10–134 km apart) located on 4 East Foundation ranches spanning the semiarid region from the Gulf Coast to western South Texas, United States (Fig. 2.2). One study site was on each of the following ranches: 1) Buena Vista in Jim Hogg County (6 113 ha; lat 26 ˚57'14.4"N, long -98˚27'21.6"W); 2) East El Sauz in Willacy County (10 984 ha; lat 26˚31'58.8"N, long -97˚29'23.9"W); and 3) Santa Rosa in Kenedy County (7 544 ha; lat 27˚10'58.8"N, long -97˚51'39.6"W). The center of the study site was the central point of the Buena Vista and Santa Rosa ranch. The study site at East El Sauz was centered in the southern portion of the ranch because the northern area of the ranch consisted of areas with active sand dunes and dense live oak mottes that were not conducive to cattle grazing and would not have met the objectives of this study. Three study sites were located on San Antonio Viejo ranch, 60 034 ha, in Jim Hogg and Starr counties with a study site in the northern (site 1; lat 27˚1'44.4"N, long -98˚47'13.2"W), central (site 2; lat 26˚53'49.2"N, long -98˚43'40.8"W), and southern (site 3; lat 26˚45'25.2"N, long -98˚46'11.9"W) portion of the ranch. Study sites within San Antonio Viejo were selected in conjunction with another study and were based on the central location of 3 separate white-tailed deer captures that occurred the previous year. I conducted this study on a landscape scale that encompassed a gradient of soils and rainfall representative of the South Texas semiarid environment.

All of the study sites, except San Antonio Viejo site 3, were in the Coastal Sand Plain ecoregion. San Antonio Viejo site 3 was in the Tamaulipan Thornscrub ecoregion. Vegetation

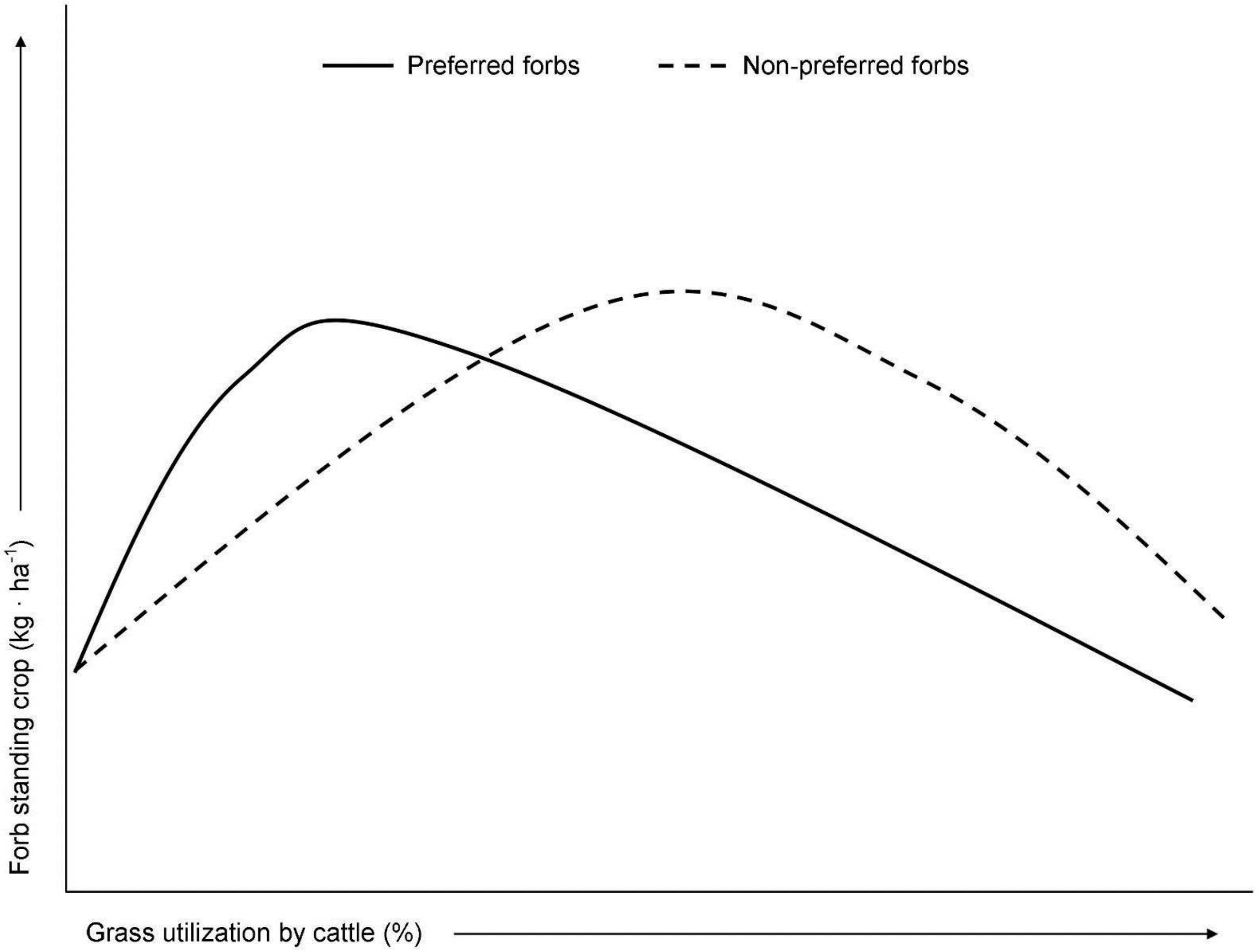

Figure 2.1. Hypothetical relationship of standing crop of preferred and non-preferred deer forbs with grass utilization by cattle.

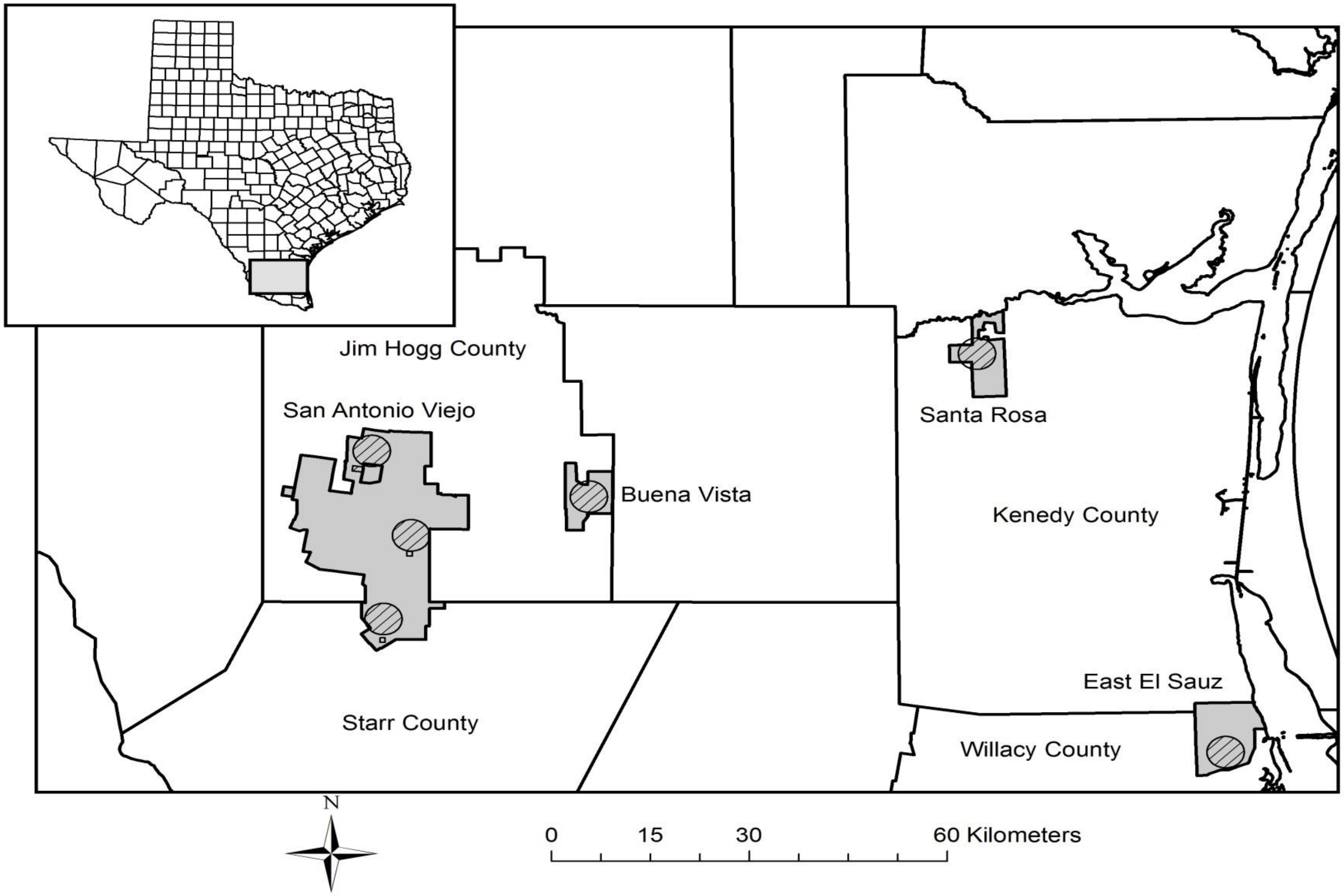

Figure 2.2. Location of six 2 500 ha study sites (circles with hatch marks; 10–134 km apart) located on 4 East Foundation ranches (gray in color) spanning the semiarid region from the Gulf Coast to western South Texas, United States.

characteristics across the landscape ranged from open grasslands with interspersed woody mottes to thornscrub woodlands. Detailed descriptions of vegetation for the Coastal Sand Plain are described in Diamond and Fulbright (1990), Forman et al. (2009), Fulbright (2001), and Fulbright et al. (1990). Detailed descriptions of the Tamaulipan Thornscrub are in Fulbright (2001).

Most study sites had predominately sandy soils, except for San Antonio Viejo site 3. More than 80% of the 2 500 ha study areas on Buena Vista, East El Sauz, Santa Rosa, and San Antonio Viejo site 1 contained soils with ≥ 82% sand. About 68% of study area on San Antonio Viejo site 2 had soils with ≥ 82% sand, while 99% of study area on San Antonio Viejo site 3 consisted of soils that comprised ≤ 58% sand (Fig. 2.3; USDA-NRCS, 2011a, 2011b). The dominate soil series at: 1) Buena Vista, San Antonio Viejo sites 1 and 2 were Nueces-Sarita association, Delmita, and Comitas (Alfisols); 2) East El Sauz were Galveston and Mustang (Alfisols and Entisols); 3) Santa Rosa were Palobia, Sauz, and Yturria (Alfisols and Entisols); and 4) San Antonio Viejo site 3 were Copita, McAllen, and Zapata (Inceptisols; USDA-NRCS, 2011a, 2011b).

Highly stochastic rainfall events and drought years are characteristic of semiarid environments. Average yearly rainfall for the region is 46.2 cm, with September expected to receive the highest monthly rainfall, 11.9 cm (Texas A&M AgriLife Research and Extension Center, 2015). Regional average annual rainfall received was 32.1 cm, 36.4 cm, and 45.8 cm during 2012, 2013, and 2014, respectively. During this study, rainfall was not only highly variable from year to year, but also fluctuated among study site locations within year (Table 2.1).

Table 2.1. Annual rainfall received (cm) during deployment of cattle grazing exclosures on 4 East Foundation ranches in South Texas, 2012–2014.

Study Site	2012	2013	2014
Buena Vista	25.4	19.1	32.5
East El Sauz	33.8	37.1	72.4
Santa Rosa	30.5	41.2	42.9
San Antonio Viejo site 1	37.3	38.4	42.9
San Antonio Viejo site 2	37.3	38.4	43.9
San Antonio Viejo site 3	40.1	42.4	40.6

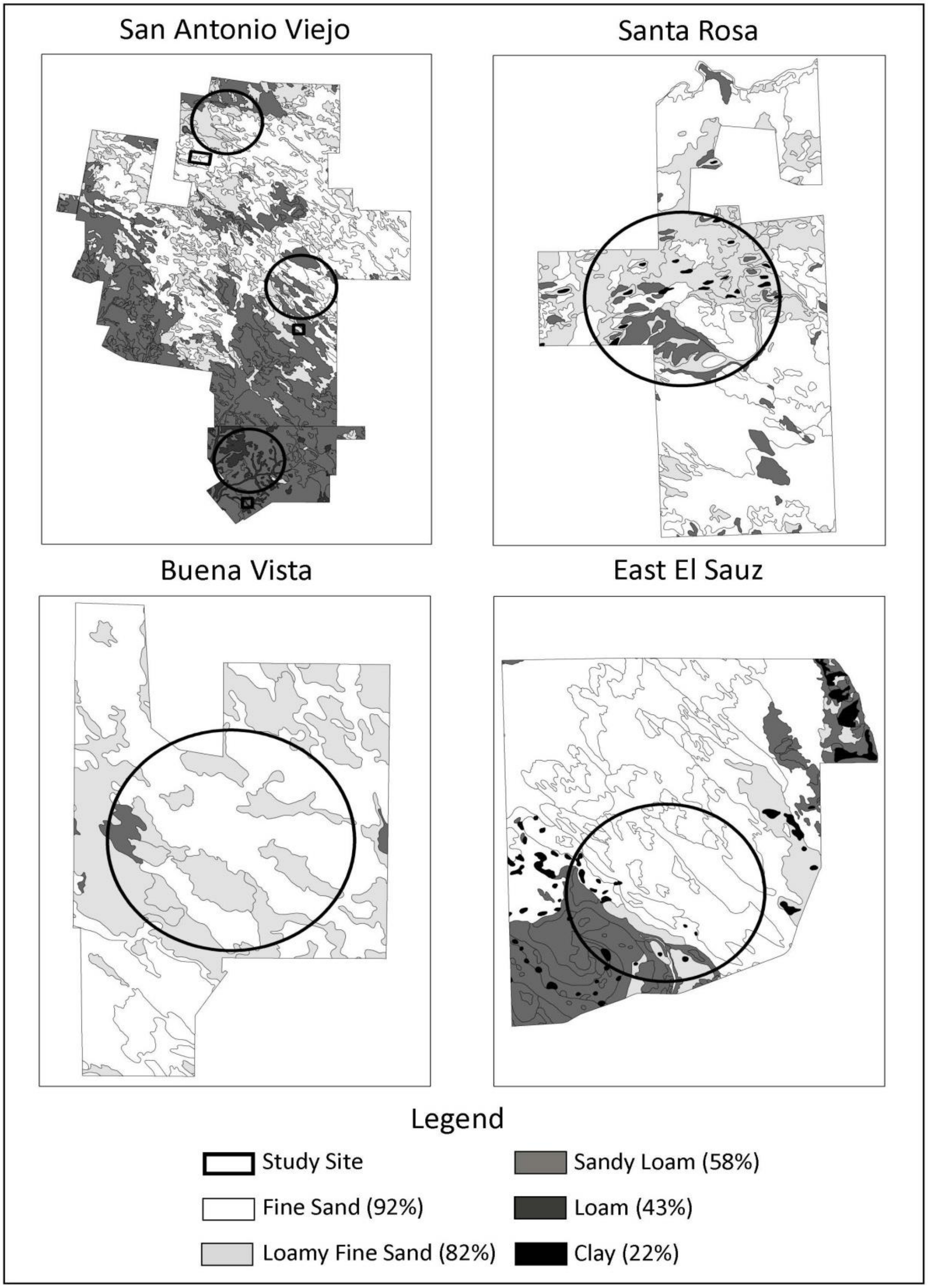

Figure 2.3. Soil texture description (percent sand composition of soil) on 4 East Foundation ranches in South Texas with the six 2 500 ha study sites defined with a bold-lined black circle.

Drought prevailed during 2 (2012 and 2013) of the 3 years of this study (Fig. 2.4; National Integrated Drought Information System-NOAA, 2015). However, most years (5 out of 11) in recent history were drought years (2006, 2009, 2011–2013), with average Palmer Drought Severity Index (PDSI) values ranging from moderate to severe drought (Fig. 2.4). Thus, this study was conducted under environmental conditions typical for South Texas semiarid environment (Diamond and Fulbright, 1990).

Grass utilization by cattle and standing crop of forbs

I installed fifty 1.5 m × 1.5 m grazing exclosures (Chambers and Brown, 1983) within each of the six 2 500 ha study sites during 28 January to 11 March 2012. I used ArcMap (ArcGIS software v. 10, ESRI, Redlands, CA) to randomly allocate each grazing exclosure, at least 100 m apart, in each of the study sites. My study objective was to determine impacts of cattle grazing grasses on forb standing crop. Cattle, white-tailed deer, and nilgai (*Boselaphus tragocamelus*) were excluded from grazing inside each grazing exclosure, but all had access to consume forages outside of each grazing exclosure. On my study sites in South Texas, graminiods constituted the highest proportion of cattle diets and greater than in deer and nilgai diets based on seasonal stable isotope analysis of ungulate diets. During autumn 2012–2014, grasses comprised 87.9% ± 1.3% ($\bar{x}$ ± 1 SE) of cattle diets compared to 10.0% ± 0.9% of deer diets and potential range of 21.0–38.0% ± 1.9% of nilgai diets (Hines et al., unpublished data). Thus grass utilization is representative of cattle grazing on my study sites. Furthermore, to determine impacts of deer and nilgai on forb standing crop, at the 3 study sites on San Antonio Viejo, I randomly allocated 10 of the 50 grazing exclosures within each of 3 cattle grazing exclosures (65–152 ha) adjacent to each 2 500 ha study site. Each cattle grazing exclosure excluded cattle but not deer and nilgai. Therefore, sampling locations within cattle grazing exclosures served as a comparison of grass

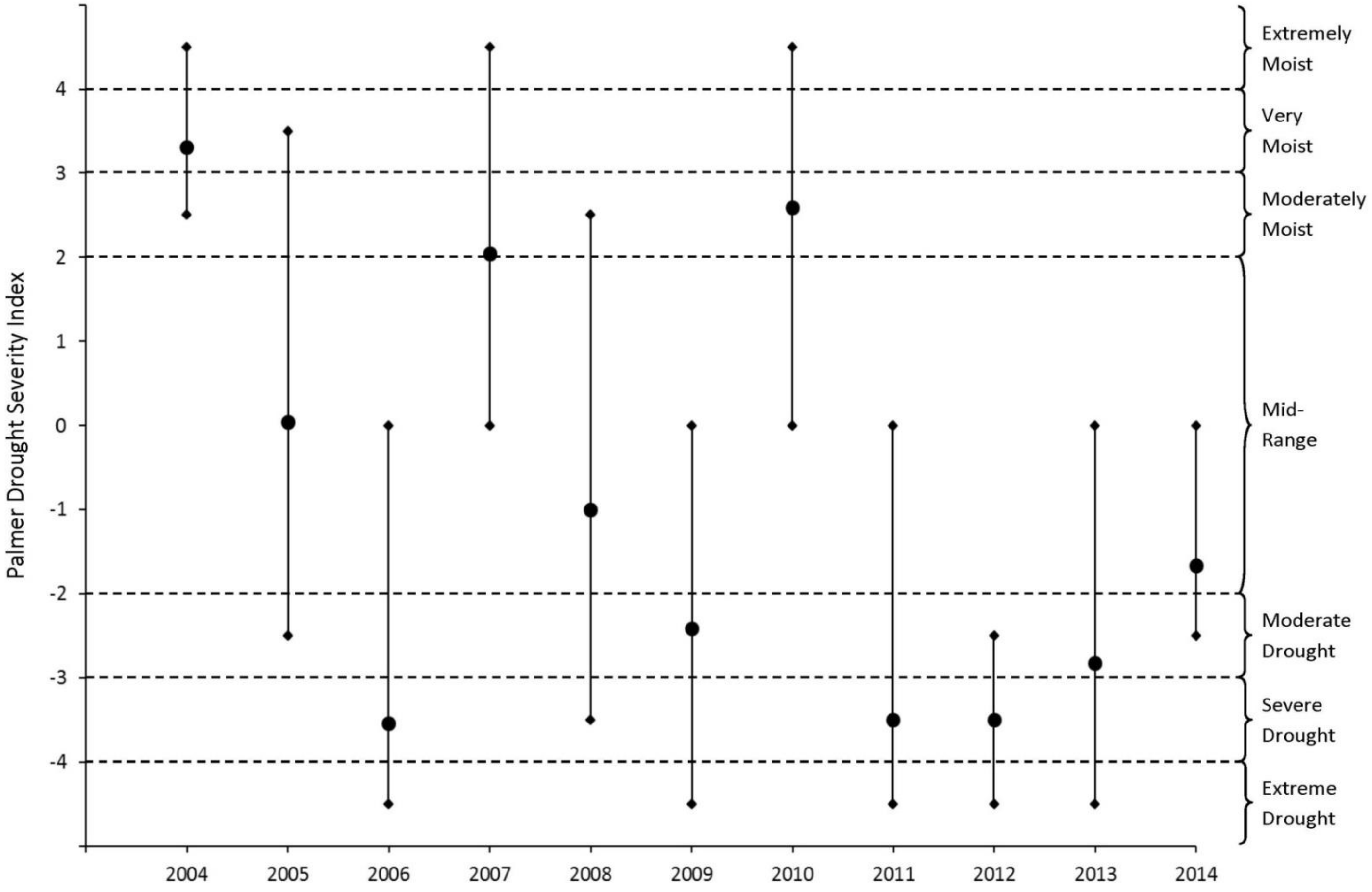

Figure 2.4. Mean annual Palmer Drought Severity Index (PDSI) values (closed circles) were calculated by averaging monthly PDSI value for each year during 2004–2014 for South Texas region in which this study was conducted (National Integrated Drought Information System-NOAA, 2015). For each year, the maximum and minimum PDSI value is graphed (closed diamonds).

utilization on forb standing crop in the absence of cattle, but in the presence of white-tailed deer and nilgai. The other ranches did not have cattle grazing exclosures at the initiation of the study.

Each grazing exclosure was constructed using 10 cm × 10 cm spacing, 6-gauge galvanized utility panels and 4 t-posts. The center of the grazing exclosure was the ungrazed sampling area. I installed each grazing exclosure in areas dominated by herbaceous vegetation. At least 10 m from each grazing exclosure, to allow adequate distance for possible vegetation trampling that might occur from curious cows inspecting the new grazing exclosure, I marked the north corner of a paired outside sampling area with a t-post (Loft et al., 1987); this was the paired grazed sampling area. I attempted to reduce environmental heterogeneity between paired sampling areas by ensuring areas were: 1) in close proximity; 2) had similar percent vegetation species and bare ground; and 3) located as similar as possible to the composition of other vegetation.

Grazing exclosures were in place for 8–12 months on each study site before samples were collected. In South Texas, most of the herbaceous forage production occurs in 2 periods, April to June and September to October; however, autumn is the only season when grasses and forbs are concurrently in their peak growing season in South Texas (Fulbright and Ortega-S., 2013). Thus, I sampled during autumn. During November–December 2012 and September–October 2013 and 2014, forage standing crop was clipped at ground level within a 0.5 × 0.5 m sampling frame placed in the center of each grazing exclosure and 0.5 m from the t-post marking the paired grazed sampling area. Within each grazing exclosure, the distance between the sampled plot and all panels was 0.5 m, which ensured standing crop of sampled forages was not disturbed by large ungulates. I was unable to control for inherent biases associated with this method, such as birds roosting on grazing exclosures (Bork and Werner, 1999).

Forage samples were separated into 1) grasses, 2) forbs preferred by deer, and 3) forbs not preferred by deer. I separated forb species into those preferred and not preferred by deer based on previous research regarding forb palatability to deer in South Texas (Folks, 2012; Gann, 2012; Grahmann, 2009). Non-preferred forbs consisted of 32 species that white-tailed deer would either not consume, or only consume as a last resort when all other forage was absent (Appendix B). Since deer are opportunistic feeders (Fulbright and Ortega-S., 2013), all other forbs were considered preferred by deer (Appendix C). Forage samples were dried at 45°C until they reached a constant mass, and then weighed to the nearest 0.1 g. After sampling was completed, grazing exclosures were moved 10 m in a randomly assigned cardinal direction (previously sampled locations were avoided) and a new paired grazed area was selected and marked.

Statistical Analyses

Each randomly allocated paired sampling location (within exclosure and grazed area) was defined as the experimental unit. I considered pairs of exclosures and associated grazed area as experimental units because in heterogeneous environments, averaging variables collected at sampling locations across larger spatial scales disregards the spatial heterogeneity that naturally occurs in semiarid environments and the resulting model may not be representative of the landscape in which the study was conducted (Bork and Werner, 1999).

First, I calculated the difference in standing crop of forbs (each for preferred, non-preferred, and total forbs) in the grazed area (the treatment) minus the standing crop of forbs in the non-grazed area (the control) for each paired sampling location because my objective was to investigate the effect of grazing versus a non-grazed area. This calculation is analogous to a paired t-test. The null hypothesis of a paired t-test is H_o: $\mu_1 = \mu_2$ (e.g., μ_1 = standing crop of forbs in the treatment and μ_2 = standing crop of forbs in paired control) is statistically equivalent to the null hypothesis of my calculation for the difference in standing crop of forbs, where H_o: $\mu_1 - \mu_2 = 0$. Hence, any value other than 0 for the difference in the standing crop of forbs (e.g., paired t-test null hypothesis would be rejected) would indicate a significant effect on the standing crop of forbs in a grazed relative to a non-grazed area. By calculating the difference in the treatment minus paired control, a positive value would indicate forb standing crop increased in the grazed area, while a negative value would indicate forb standing crop decreased in the grazed area. This calculation accounted for spatial variability associated with vegetation communities across the landscape by computing a relative value that compared paired areas that had similar vegetation and were exposed to similar environmental conditions (e.g., comparing treatment to a paired control within close proximity; Bork and Werner, 1999).

Secondly, for each of my paired grazing exclosure locations, I estimated relative grass utilization (e.g., to examine if grass utilization releases competitive advantage allowing standing crop of forbs to increase). This relative utilization metric was used because my objective was to determine the impact of grass utilization (e.g., herbivory) on standing crop of forbs (Bork and Werner, 1999). I calculated percent grass utilization (GU) in a grazed area compared to its paired ungrazed area as:

$$GU\ (\%) = [\frac{(I - O)}{I}]\ *\ 100.$$

Where I is the standing crop of grass in the grazing exclosure (the control) and O is the standing crop of grass in the grazed sampling area (the treatment). I estimated a utilization value for each sampling location, which accounted for spatial variability associated with vegetation communities (Bork and Werner, 1999) and patchiness of grazing across the landscape (Andrew, 1988; Landsberg et al., 2003, 1999; Pringle and Landsberg, 2004) by computing a relative value that compared paired areas with similar vegetation and were exposed to similar environmental conditions.

Grass utilization, when there is greater standing crop of grass in the grazing exclosures compared to the paired grazed area, is bound between 0–100%. However, when standing crop of grass is greater in the grazed area compared to the paired grazing exclosure, negative grass utilization values could be infinite. This occurred at one-fifth of the paired sampling locations (*n* = 176) during this study. Larger standing crop of grass in the grazed area could have occurred by pure chance or other factors such as compensatory growth in response to grazing (McNaughton, 1984, 1979; Oba et al., 2001), which has been documented for drought-tolerant grass under water stress conditions (Georgiadis et al., 1989; von Staalduinen and Anten, 2005). Therefore, negative utilization values could have biological meaning. I scaled negative utilization values so they were bound between -100–0% and retained these negative values in my regression models.

Retaining the full suite of utilization values applies more biological meaning to a relative calculation by including the entire gradient of grass comparisons which were present at paired sampling locations across the semiarid landscape. For example: 1) -100% cattle grazing utilization is representative of 100% more grass in the grazed area compared to its paired non-grazed area; 2) 0% cattle grazing utilization is representative of equal standing crop of grass in the paired areas; and 3) 100% cattle grazing utilization is representative of 100% less grass in the grazed area compared to its paired non-grazed area. By including negative grass utilization values, I was able to compare paired sampling locations where there was a higher standing crop of grasses in the treatment area (e.g., grazed area) relative to the control (e.g., non-grazed area). Furthermore, the inclusion of negative values is: 1) more representative of heterogeneity associated with vegetation communities in semiarid arid systems; 2) does not bias utilization estimates (e.g., overestimating degree of grass herbivory) by zeroing out data; and 3) does not bias the statistical analysis employed to investigate the relationship among paired samples because it is analogous to a directionally-neutral test (e.g., two-tailed test examining normal distribution of population), whereas beginning at 0% utilization (e.g., removing all negative values from the data set) is analogous to only examining a portion of the population, such as when employing a one-tailed statistical test (Bork and Werner, 1999). The inclusion of the negative utilization values and the use of relative calculations (e.g., both percent utilization and dependent variable used in my models) provided a more robust, yet conservative analysis, to examine the impact of grass utilization on standing crop of forbs (Bork and Werner, 1999).

Finally, I wanted to determine if the difference in the standing crop of forbs was related to variation in grass utilization. My dependent variable in the model was the difference in standing crop of forbs between the grazed plots and exclosures; a separate model for each preferred, non-preferred, and total (preferred + non-preferred) forbs. I maintained my paired study design by analyzing the condensed paired t-test (one response variable representing the difference between pairs) in each regression model. The independent variable in each model was grass utilization. In each model, I included variables (subsequently listed) documented to influence standing crop of vegetation, thus allowing me to determine if grass utilization was related to standing crop of forbs after accounting for their influence on vegetation standing crop (e.g., Type III sums of squares test); I included: 1) year as a random effect because vegetation communities can vary temporally (Bork and Werner, 1999); 2) percent sand as a continuous variable representative of soil texture at each sampling location (USDA-NRCS, 2011a, 2011b); 3) autumn (August and September) rainfall received at each 2 500 ha study site obtained from weather stations located within each study site on Buena Vista, East El Sauz, and Santa Rosa and within 4.5–9.5 km of study sites on San Antonio Viejo ranch (Texas A&M AgriLife Research and Extension Center, 2015); 4) a linear combination variable, determined from principle components analysis (Proc Princomp, SAS, version 9.3, SAS Institute, Cary, NC, USA), of daily minimum and maximum temperature averaged across August–September and average daily temperature during August–September obtained from aforementioned weather stations as covariates because these are principal environmental factors influencing vegetation (Fulbright et al., 2008; Georgiadis et al., 1989; Krausman et al., 2009; Walker and Wilson, 2002; Vavra, 2005); and 5) distance from each grazing exclosure to nearest water source determined using near analysis tool in ArcMap as a covariate because it influences cattle grazing impacts on vegetation (Landsberg et al., 2003, 1999; Pringle and Landsberg, 2004). The 3 individual temperature variables were collinearly related, thus instead, a linear combination variable that retained 78% of variation of 3 temperature variables was included in each model so not to bias model results (Aguilera et al., 2006). There was no multicollinearity among predictor variables for each of my models (condition index < 17.6; Haque et al., 2002). I used mixed models because I had both random and fixed effects in my model (Proc Mixed; SAS, 2016).

To pass normality and homogeneity of variances, the difference in standing crop for each forb category was log transformed. I report back-transformed values in the results. Back-transformed log effect sizes (or estimated β) are interpreted as the multiplicative change on the median difference in forb standing crop with each 1% change in grass utilization. Since e^{β} is roughly equal to $1 + \beta$ for small values, the reported effect size is an approximated percent change in the median difference in forb standing crop for every 1% increase in grass utilization.

Mitchell and Wass (1996) pointed out that modeling standing crop of forage, calculated as forage inside an exclosure minus grazed area divided by time, as a function of grazing utilization, relative calculation of standing crop of forage consumed in grazed area relative to available forage standing crop in the non-grazed area, would have no relationship to consumption of forage by herbivores because the slope of the model would be ungrazed forage standing crop per unit time. However, because I am modeling the difference in forb standing crop as a function of grass utilization, the slope of my model in the simplest form is the median difference in standing crop of forbs (in a grazed area relative to paired non-grazed area) per standing crop of grass in the grazed area.

Paired sampling locations were excluded from the analyses when: 1) grazing exclosure panels were compromised allowing ungulates to graze inside exclosure; 2) sampling areas were flooded; and 3) when there was no grass in the grazing exclosure (cannot divide by zero).

Results

Across all sites and years (except East El Sauz during 2013), herbaceous forage standing crop (total forbs + grasses) inside 1.5 m × 1.5 m grazing exclosures averaged across all sampling locations for each site and year of study was 152–2 465 kg · ha^{-1} below potential range production estimated by NRCS (weighted average, by area for each site, determined from the ecological site description for soil series within each site; Table 2.2). Across the study region during 2012–2014, grass utilization ($\bar{x}$ ± 1 SE) was 44.1 ± 2.1% (ranged -100–100%; *n* = 707; Table 2.3). During 2012–2014, grass utilization ($\bar{x}$ ± 1 SE) within cattle grazing exclosures (65–152 ha sites at San Antonio Viejo ranch) was 30.9 ± 5.7% (ranged -79–100%; *n* = 85; Table 2.3). Mean grass utilization by deer and nilgai within cattle grazing exclosures (65–125 ha sites) was within expected range based on stable isotope analysis of deer and nilgai diets during autumn, with deer and nilgai diets consisting of 10.0% ± 0.9% and 21.0–38.0% ± 1.9% grasses, respectively (Hines et al., unpublished data).

Table 2.2. Mean standing crop (± 1 SE in $\text{kg} \cdot \text{ha}^{-1}$) of preferred and non-preferred deer forbs and grasses inside (non-grazed) and outside (grazed) the 1.5 m × 1.5 m grazing exclosure within 2 500 ha study sites and within the 65–152 ha cattle grazing exclosure sites (cattle were excluded, but not deer and nilgai) on San Antonio Viejo ranch (SAV site # CE), on 4 East Foundation ranches in South Texas, autumn 2012–2014. Standing crop was averaged across 1.5 m × 1.5 m grazing exclosure sampling sites (*n*) for each site and year. Across all sites and years (except East El Sauz during 2013), average herbaceous forage standing crop (total forbs + grasses) inside grazing exclosures were 152–2 465 $\text{kg} \cdot \text{ha}^{-1}$ below NRCS potential range production.

Site	*n*	Preferred forbs Inside	Preferred forbs Outside	Non-preferred forbs Inside	Non-preferred forbs Outside	Grasses Inside	Grasses Outside	[1]NRCS range production
2012								
Buena Vista	36	67 ± 15	27 ± 8	146 ± 30	88 ± 21	177 ± 49	71 ± 16	2 158 ± 82
East El Sauz	44	272 ± 81	91 ± 21	326 ± 129	204 ± 66	801 ± 140	209 ± 40	1 639 ± 10
Santa Rosa	41	101 ± 28	34 ± 16	109 ± 31	48 ± 19	412 ± 75	61 ± 12	2 195 ± 6
San Antonio Viejo 1	37	114 ± 19	41 ± 10	228 ± 46	133 ± 27	552 ± 122	115 ± 37	1 649 ± 19
SAV site 1 CE	10	185 ± 34	233 ± 53	80 ± 43	139 ± 64	1 507 ± 458	760 ± 272	2 000 ± 262
San Antonio Viejo 2	31	112 ± 25	34 ± 11	292 ± 67	154 ± 32	282 ± 54	18 ± 6	1 786 ± 22
SAV site 2 CE	6	256 ± 66	49 ± 28	418 ± 150	376 ± 101	162 ± 86	8 ± 5	988 ± 63
San Antonio Viejo 3	26	44 ± 27	1 ± 1	[2]0	[2]0	1 400 ± 675	114 ± 37	1 652 ± 39
SAV site 3 CE	10	8 ± 7	38 ± 38	[2]0	[2]0	1 204 ± 432	911 ± 300	2 019 ± 239

[1] NRCS range production is the weighted (by area) average (± 1 SE in $\text{kg} \cdot \text{ha}^{-1}$) of potential range production based on ecological site description for soil series within each study site during unfavorable years- when growing conditions are below average (2012–2013 PDSI drought years; see Fig. 2.4, pg. 28) and during normal years- when growing conditions are average (2014 PDSI mid-range year; see Fig. 2.4, pg. 28).

[2] Value was $\leq 0.7\ \text{kg} \cdot \text{ha}^{-1}$.

Table 2.2. Continued.

		Preferred forbs		Non-preferred forbs		Grasses		[1]NRCS range production
Site	*n*	Inside	Outside	Inside	Outside	Inside	Outside	
2013								
Buena Vista	42	346 ± 58	197 ± 39	588 ± 83	520 ± 67	178 ± 53	77 ± 30	2 158 ± 82
East El Sauz	46	498 ± 77	508 ± 115	688 ± 179	443 ± 74	912 ± 138	371 ± 77	1 639 ± 10
Santa Rosa	46	502 ± 135	289 ± 59	614 ± 110	396 ± 73	521 ± 94	253 ± 50	2 195 ± 6
San Antonio Viejo 1	38	250 ± 37	243 ± 49	69 ± 36	25 ± 14	175 ± 26	74 ± 17	1 649 ± 19
SAV site 1 CE	10	278 ± 89	286 ± 71	88 ± 52	172 ± 81	1 189 ± 273	626 ± 165	2 000 ± 262
San Antonio Viejo 2	39	243 ± 66	194 ± 35	137 ± 41	136 ± 42	189 ± 40	147 ± 33	1 786 ± 22
SAV site 2 CE	10	342 ± 108	234 ± 77	52 ± 38	101 ± 100	290 ± 157	82 ± 14	988 ± 63
San Antonio Viejo 3	35	65 ± 36	11 ± 5	[2]0	[2]0	1 148 ± 238	620 ± 136	1 652 ± 39
SAV site 3 CE	10	142 ± 86	92 ± 77	[2]0	[2]0	655 ± 206	424 ± 154	2 019 ± 239
2014								
Buena Vista	49	764 ± 96	806 ± 123	91 ± 33	75 ± 21	803 ± 126	512 ± 82	3 813 ± 140
East El Sauz	41	418 ± 63	498 ± 97	265 ± 77	185 ± 52	1 716 ± 194	638 ± 77	2 671 ± 16
Santa Rosa	49	480 ± 200	297 ± 48	73 ± 40	77 ± 51	2 240 ± 236	1 514 ± 220	3 661 ± 9
San Antonio Viejo 1	38	556 ± 68	492 ± 58	50 ± 16	136 ± 50	978 ± 113	835 ± 85	3 114 ± 34
SAV site 1 CE	10	722 ± 179	415 ± 109	10 ± 6	285 ± 184	1 827 ± 381	1 060 ± 292	3 695 ± 445
San Antonio Viejo 2	38	257 ± 37	215 ± 32	15 ± 14	54 ± 40	621 ± 98	460 ± 152	3 358 ± 37
SAV site 2 CE	10	354 ± 102	182 ± 27	[2]0	1 ± 1	345 ± 74	294 ± 71	2 077 ± 91
San Antonio Viejo 3	31	59 ± 21	55 ± 16	57 ± 48	[2]0	1 122 ± 189	916 ± 194	3 056 ± 76
SAV site 3 CE	9	28 ± 27	6 ± 4	0	0	1 405 ± 296	1 434 ± 344	3 279 ± 353

[1] NRCS range production is the weighted (by area) average (± 1 SE in kg · ha^{-1}) of potential range production based on ecological site description for soil series within each study site during unfavorable years- when growing conditions are below average (2012–2013 PDSI drought years; see Fig. 2.4, pg. 28) and during normal years- when growing conditions are average (2014 PDSI mid-range year; see Fig. 2.4, pg. 28).

[2] Value was ≤0.7 kg · ha^{-1}.

Table 2.3. Mean (± 1 SE), minimum, and maximum values of grass utilization (%), relative calculation for each paired non-grazed and grazed sampling location, for each 2 500 ha study site and each 65–152 ha cattle grazing exclosure site (cattle were excluded, but not deer and nilgai) on San Antonio Viejo ranch (SAV site # CE), on 4 East Foundation ranches in South Texas, autumn 2012–2014. Percent grass utilization was averaged across paired (non-grazed area within the 1.5 m × 1.5 m grazing exclosure and grazed area) sampling sites (*n*) for each site and year.

Site	*n*	Mean	Minimum	Maximum
2012				
Buena Vista	36	42 ± 10	-63	100
East El Sauz	44	65 ± 7	-91	100
Santa Rosa	41	76 ± 6	-57	100
San Antonio Viejo 1	37	65 ± 8	-61	100
SAV site 1 CE	10	36 ± 16	-75	95
San Antonio Viejo 2	31	86 ± 7	-64	100
SAV site 2 CE	6	92 ± 6	65	100
San Antonio Viejo 3	26	85 ± 4	25	100
SAV site 3 CE	10	13 ± 22	-79	100
2013				
Buena Vista	42	44 ± 10	-78	100
East El Sauz	46	56 ± 7	-97	100
Santa Rosa	46	47 ± 8	-71	100
San Antonio Viejo 1	38	54 ± 9	-100	100
SAV site 1 CE	10	31 ± 19	-59	94
San Antonio Viejo 2	39	14 ± 10	-85	100
SAV site 2 CE	10	38 ± 15	-42	94
San Antonio Viejo 3	35	30 ± 10	-70	100
SAV site 3 CE	10	29 ± 14	-52	96
2014				
Buena Vista	49	17 ± 8	-87	100
East El Sauz	41	53 ± 7	-77	100
Santa Rosa	49	29 ± 7	-67	100
San Antonio Viejo 1	38	3 ± 7	-55	84
SAV site 1 CE	10	47 ± 11	-14	93
San Antonio Viejo 2	38	27 ± 10	-83	100
SAV site 2 CE	10	27 ± 17	-57	100
San Antonio Viejo 3	31	22 ± 11	-94	100
SAV site 3 CE	9	-12 ± 12	-56	49

Averaged across study sites and years, the standing crop of preferred forbs ($\bar{x}$ ± 1 SE) inside 1.5 m × 1.5 m grazing exclosures (ungrazed area) was 293 ± 50 kg · ha^{-1} and outside grazing exclosures (grazed area) was 227 ± 52 kg · ha^{-1} (Table 2.2, pg. 36). The difference in standing crop of preferred forbs was positively ($P < 0.002$) related to grass utilization; there was a 0.9% increase in the difference in standing crop of preferred forbs for every 1% increase in grass utilization, (Table 2.4; Fig. 2.5). While statistically significant, this represented an increased preferred forb standing crop in the grazed treatment (compared to control) of only 0.5 kg · ha^{-1}at 100% grass removal. In the absence of cattle (e.g., sampling locations within cattle grazing exclosures where deer and nilgai could access), the difference in standing crop of preferred forbs was not related ($P = 0.485$) to grass utilization. Averaged across study sites and years in the absence of cattle, the standing crop of preferred forbs inside 1.5 m × 1.5 m grazing exclosures (ungrazed area) was 260 ± 38 kg · ha^{-1} and outside grazing exclosures (grazed area) was 178 ± 25 kg · ha^{-1} (Table 2.2, pg. 36).

Averaged across study sites and years, the standing crop of non-preferred forbs ($\bar{x}$ ± 1 SE) inside 1.5 m × 1.5 m grazing exclosures was 206 ± 52 kg · ha^{-1} and outside grazing exclosures was 153 ± 36 kg · ha-1 (Table 2.2, pg. 36). The difference in standing crop of non-preferred forbs was not related to grass utilization in the presence of cattle ($P = 0.269$; Table 2.4; Fig. 2.5) or in the absence of cattle ($P = 0.947$). Averaged across study sites and years in the absence of cattle, the standing crop of non-preferred forbs ($\bar{x}$ ± 1 SE) inside 1.5 m × 1.5 m grazing exclosures was 57 ± 17 kg · ha^{-1} and outside grazing exclosures was 109 ± 30 kg · ha-1 (Table 2.2, pg. 36).

When preferred forbs and non-preferred forbs were combined and analyzed as total forbs, the approach used by past researchers, the difference in standing crop of total forbs was positively related ($P < 0.001$) to grass utilization; for every 1% increase in grass utilization, there was a 1.2% increase in the difference in standing crop of total forbs (Table 2.4; Fig. 2.5). While statistically significant, this represented an increased total forb standing crop in the grazed treatment of only 0.7 kg · ha^{-1}at 100% grass removal. In the absence of cattle, the difference in standing crop of total forbs was not related ($P = 0.575$) to grass utilization.

Table 2.4. Models for the difference in the median forb standing crop (ŷ; grazed minus paired non-grazed area) and grass utilization by cattle (CGU; *n* = 792 paired areas) with covariates (percent sand composition of soil texture- S, autumn (August–September) rainfall received- R, distance to nearest water source- W, linear combination of temperature- T) on 4 East Foundation ranches in South Texas, 2012–2014. I used Proc Mixed (SAS v.9.3), with year included as a random effect, for each model (preferred, non-preferred, and total forbs).

Forb Category	Model	[1]*P*
Preferred deer forbs	ŷ = e^(-1.3032 + 0.0009*CGU + -0.0101*S + 0.0433*R + 0.0002*W + 0.0582*T)	0.0015
Non-preferred deer forbs	ŷ = e^(-1.277 + 0.0028*CGU + 0.0128*S + -0.0199*R + 0.0001*W + 0.2116*T)	0.2685
[2]Total forbs (preferred + non-preferred)	ŷ = e^(-3.4018 + 0.0128*CGU + 0.0154*S + 0.0167*R + 0.0003*W + 0.3478*T)	< 0.0001

[1] Grass utilization estimate *P* value.

[2] Not separating forbs, based on preference by a species, is the approach used in past research.

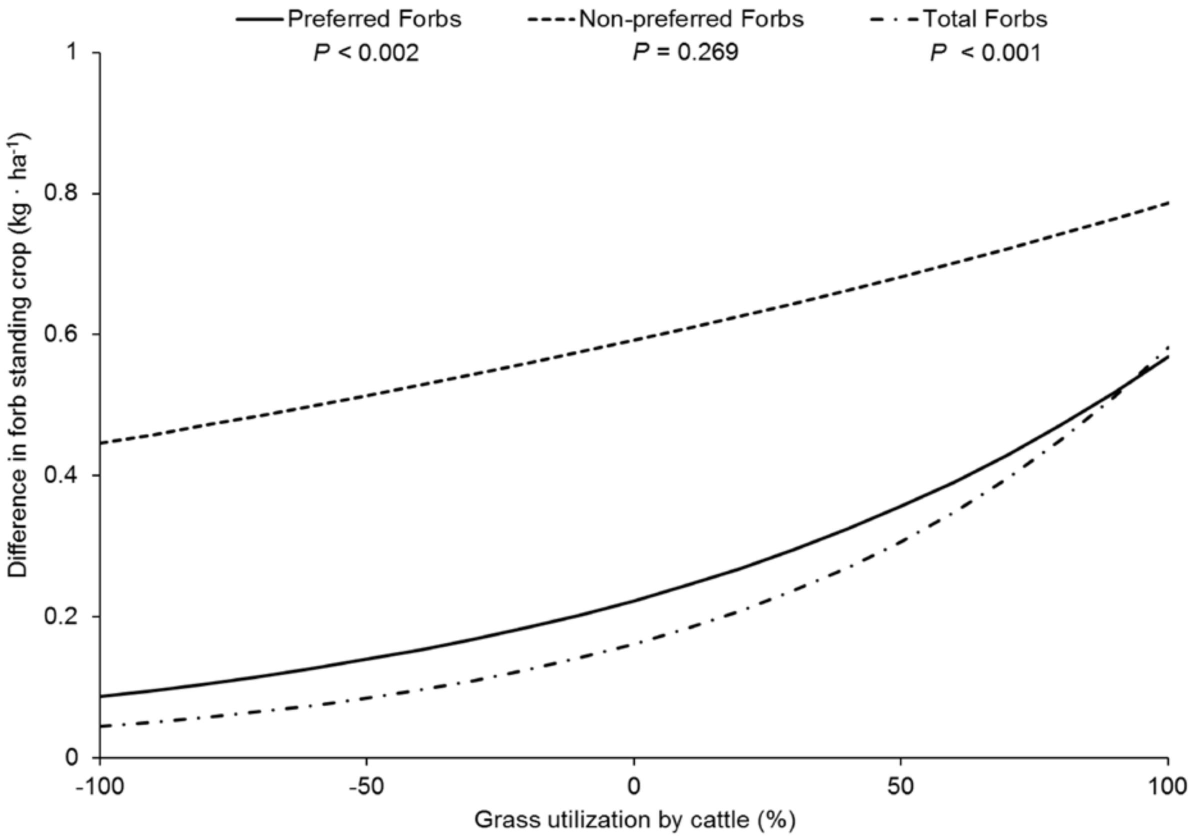

Figure 2.5. The difference in standing crop (grazed minus paired non-grazed area) of preferred and non-preferred deer forbs and difference in total forbs (preferred + non-preferred) as it relates to grass utilization by cattle across years (2012–2014) on 4 East Foundation ranches in South Texas. The difference in forb standing crop for each preference category was log transformed, therefore the relationship graphed has been back transformed from log scale and is the median difference in standing crop of forbs as it relates to grass utilization, while holding covariates constant (median value). The median value of non-preferred deer forbs was larger than preferred forbs because the range of values for the difference in non-preferred forbs was smaller. Therefore, when non-preferred and preferred forbs were combined, the median value for the difference in total forbs was lower than the median values of the difference in forb standing crop when separated by preference categories. See Table 2.4 (pg. 40) for models.

Discussion

My hypotheses were not supported. The increased standing crop of forbs (preferred and total) in the grazed treatment, relative to the control, as a result of grass utilization by cattle was biologically insignificant; the statistical relationship determined from my models was most likely an artifact of my large sample size. In addition, the response of non-preferred forbs was different from preferred forbs, but these different responses were masked when forb preference categories were combined (e.g., emulating previous research methods). Forb response across the semiarid landscape of South Texas, under the conditions in which I conducted this study, is not biologically affected by cattle utilization of grasses.

I did not observe an increase in forbs in response to grass utilization. There are several potential reasons for this. First, the hypothesis that forbs will increase when cattle consume grasses is based on having a climax or near climax grassland dominated by grasses with few forbs present (Holechek et al., 2011). The grasslands in this study were in early seral stage as evidenced by their low standing crop relative to potential range production. Consequently, higher successional grassland where I would expect forbs to increase in response to grass utilization by cattle did not exist in my study.

A second reason I did not observe a significant impact on forb standing crop as a result of grass utilization could be because the vegetation species on my study sites may be resistant to grazing. There is well over a century of heavy grazing by domestic livestock (e.g., cattle, sheep, goats, horses) in the region in which I conducted my study (Fulbright et al, 1990; Lehmann, 1969). For example, it was recorded in historical documents there were 1.6 million sheep on lands south of the Nueces River during the mid 1860s (e.g., South Texas region in which this study was conducted; Lehmann, 1969).

A third reason I did not observe the hypothesized response of forbs to grass utilization is that my study areas were in a semiarid region with extreme variability in precipitation. The average coefficient of variation (CV) in interannual rainfall for 2012–2015 across study sites was 34%. Several researchers have suggested that coupling between herbivores and vegetation dynamics is weak in environments with high (>33%) interannual CV in precipitation (Ellis and Swift, 1988; Von Wehrden et al., 2012). Standing crop of herbaceous vegetation in these systems is controlled by variation in rainfall and weakly influenced by herbivores (Ellis and Swift 1988). In the highly variable semiarid environment of South Texas, abiotic factors may have a larger influence on standing crop of forbs than disturbance by cattle grazing (Fulbright and Ortega-S., 2013; Leopold, 1933; Lyons and Wright, 2003; Ortega-S. et al., 2013).

My results support a hypothesis proposed by Fulbright et al. (2008); applying disturbance to cause retrogression in succession (e.g., cattle grazing decrease grasses in climax grassland) will have little effect on rangelands that are in an early-seral successional stage when both site productivity and precipitation are below a certain threshold. The literature supports the use of cattle grazing as a management tool to increase forbs because in mesic environments (typically more stable climate) with climax grasslands, many studies reported an increase in forbs in response to moderate grazing (e.g., Thill and Martin, 1989, 1986; Towne et al., 2005). But in semiarid and arid environments, reports of an increase in forbs in response to grazing are less common (e.g., Holechek et al., 2006, Ruthven et al., 2007). I determined from my landscape scale study, conducted under environmental (Diamond and Fulbright, 1990; Fulbright et al., 1990) and rangeland conditions representative of 81% of Texas rangelands (Fulbright and Ortega-S., 2013), that forb response is not estimable by biotic factors (e.g., cattle grazing grasses). Even though grass utilization may not affect forb standing crop in semiarid ecoregions, excessive grazing has negative consequences, such as reduced water infiltration (Abdel-Magid et al., 1987) and increased soil compaction (Van Havern, 1983). Accordingly, as suggested by Holechek et al. (2011), managers in semiarid environments, where forage response is controlled more by unpredictable abiotic factors (Ellis and Swift, 1988), should practice light to conservative grazing practices to sustain rangeland integrity and financial returns from both wildlife operations and livestock production.

CHAPTER III

LARGE HERBIVORE IMPACTS ON SPECIES RICHNESS IN A SEMIARID LANDSCAPE

Introduction

Conservation of biological diversity on rangelands, which comprise one-third of earth's terrestrial surface (Briske et al., 2015), is of high ecological and economic importance. Sustainability of rangelands is positively related to biodiversity (Groom et al., 2006), which benefits the health and production of large herbivores (Wang et al., 2010). Rangelands not only support the livelihood of millions of humans through domestic livestock grazing (Asner et al., 2004; Sayre et al., 2013), they also provide crucial habitat for wildlife. Eighty-four percent of mammal species in the US spend at least part of their time on rangelands (Hart, 1994). Grazing by large herbivores, both domestic and wild, influences variation in biological diversity (Grime 1973; Connel, 1978; Frank, 2005) and has become a topic of considerable interest in ecological literature. Yet the relationship between intensity of herbivory and plant species richness, an indicator of biodiversity on rangelands, widely varies in the literature (Grainger, 1992; Olff and Ritchie, 1998; Zervas, 1998), resulting in a lack of consistent theory (Danell and Bergström, 2002).

The hypothesized relationship between plant species richness and grazing by large herbivores differs depending on climate. In mesic environments, hump-back shaped species richness-herbivore relationships may be more common (Poyry et al., 2006; Yan et al., 2015) than in drier environments (Milchunas et al., 1988; Baaker et al., 2006). In semiarid systems, Milchunas and Lauenroth (1993) hypothesized the species richness-herbivore relationship would be negative (slightly unimodal; small peak followed by a rapid decline) or relatively flat (e.g., unrelated to herbivore grazing utilization). Different hypothesized relationships in semiarid environments may be due to environmental factors (e.g., rainfall, temperature, soils) and site productivity (Baaker et al., 2006; Olff and Ritchie, 1998).

Semiarid environments are subject to prolonged droughts and extreme temperatures (Walker and Wilson, 2002); therefore, researchers have suggested disturbance by large herbivores will have little impact on species richness because abiotic factors are the main driver of vegetation dynamics (e.g., non-equilibrium dynamics; Diaz et al., 2007; Ellis and Swift, 1988). Because of conflicting results (e.g., herbivore versus environmental factors) in semiarid landscapes, other researchers have suggested site productivity (e.g., commonly measured as above ground standing crop) as an important indicator deeming when large herbivores will and will not influence the vegetation community (Frank, 2005, Burns et al., 2009), but have indicated studies investigating the herbivore in conjunction with site productivity are lacking in published literature (Oba et al., 2001).

My objective was to determine the relationship between intensity of use of herbaceous vegetation by herbivores and plant species richness. Species richness may be influenced solely by environmental factors (e.g., non-equilibrium vegetation dynamics; Diaz et al., 2007; O'Connor, 1991; Walker and Wilson, 2002; Westoby et al., 1989), or in conjunction with site productivity (e.g., standing crop of herbaceous vegetation; Bakker et al., 2006; Burns et al., 2009; Frank 2005; Oba et al., 2001) or large herbivores (Eby et al., 2014; Hickman et al., 2014; Yan et al., 2015) as a monotypic or unimodal relationship (Mackey and Currie, 2000, 2001), or all aforementioned factors (Olff and Ritchie, 1998). Therefore, I also compared competing models to determine the influence of rainfall, temperature, soil texture, and potential herbaceous standing crop (e.g., representative of site productivity at time of sampling) on plant species richness as well as herbivores and investigated which variable was most influential on plant species richness.

Methods

Study site description

I selected six 2 500 ha study sites (10–134 km apart) located on 4 East Foundation ranches spanning the semiarid region from the Gulf Coast to western South Texas, USA (Fig. 2.2, pg. 23). There was one study site on each of the following ranches: 1) Buena Vista in Jim Hogg County (6 113 ha), 2) East El Sauz in Willacy County (10 984 ha), and 3) Santa Rosa in Kenedy County (7 544 ha). Three study sites were located on San Antonio Viejo, 60 034 ha, in Jim Hogg and Starr counties with a study site in the northern (site 1), central (site 2), and southern (site 3) portion of the ranch. The 2 500 ha study sites within each ranch were chosen: 1) based on the center of the ranch (Buena Vista and Santa Rosa); 2) based on the center, southern portion of ranch (East El Sauz) to avoid active sand dunes and dense live oak mottes because these are not conductive to all large herbivores (e.g., domestic cattle) utilizing the area; and 3) in conjunction with another study based on the central location of 3 separate white-tailed deer captures (3 sites on San Antonio Viejo) that occurred the previous year. In addition, there were 3 cattle grazing exclosures (65–152 ha) adjacent to each 2 500 ha study site on San Antonio Viejo ranch.

Most study sites were located in the Coastal Sand Plain ecoregion. However, San Antonio Viejo site 3 and adjacent cattle grazing exclosure were located in the Tamaulipan Thornscrub ecoregion. The Coastal Sand Plain ecoregion consists of mostly open grasslands with interspersed woody mottes and predominately sandy soils (≥ 80 % sand; dominate soil series were Nueces-Sarita association, Delmita, and Comitas (Alfisols) and Galveston, Mustang, Palobia, Sauz, and Yturria (Alfisols and Entisols); NRCS, 2011a, 2011b) while the Tamaulipan

Thornscrub ecoregion consists of thicker, thornscrub woodlands, with lower percentage of sand (≤ 58% sand; dominate soil series were Copita, McAllen, and Zapata (Inceptisols); USDA-NRCS, 2011a, 2011b) in the soils (Fig. 2.3, pg. 26). Predominant vegetation species in the study region are associated with disturbance (Diamond and Fulbright, 1990). There is a long history, at least since the mid 1860s, of heavy grazing by domestic livestock, such as cattle, sheep, goats, and horses (Fulbright et al, 1990; Lehmann, 1969). Detailed descriptions of vegetation for the Coastal Sand Plain are described in Diamond and Fulbright (1990), Forman et al. (2009), Fulbright (2001), and Fulbright et al. (1990). Detailed descriptions of the Tamaulipan Thornscrub are in Fulbright (2001).

Cattle and deer were present on all study sites. Across the study region during 2013–2015, population density estimates for cattle ranged from 13.3–21.9 cattle km^{-2} and for white-tailed deer ranged from 8.2–13.3 deer km^{-2} (Annala, 2015). However, nilgai are mostly constrained to the eastern portion of South Texas. Nilgai were prevalent on East El Sauz and Santa Rosa ranches with a small population of nilgai at San Antonio Viejo ranch that occupied the northern area of the ranch (site 1). However, during winter 2015, nilgai may have utilized vegetation at San Antonio Viejo site 3, because I found three separate nilgai fecal deposits within this study site. Nilgai density estimates during 2013–2015 for Santa Rosa and East El Sauz ranged from 4.3–10.5 nilgai km^{-2}; no density estimates for nilgai are available for San Antonio Viejo ranch because nilgai densities were too low for estimates to be made (Annala, 2015).

Herbivore utilization and species richness

I used ArcMap (ArcGIS software v. 10, ESRI, Redlands, CA) to randomly allocate locations to install fifty 1.5 m × 1.5 m grazing exclosures (Chambers and Brown, 1983), at least 100 m apart, within each of the six 2 500 ha study sites during 28 January to 11 March 2012. The objective of this study was to determine large herbivore impacts on species richness; therefore, I constructed each grazing exclosure using 10 cm × 10 cm spacing, 6-gauge galvanized utility panels and 4 t-posts, which protected vegetation from grazing by large herbivores (e.g., cattle, deer, and nilgai) but not small herbivores. At the 3 study sites on San Antonio Viejo, I randomly allocated 10 of the 50 grazing exclosures within each of 3 cattle grazing exclosures (65–152 ha) adjacent to each 2 500 ha study site to provide a comparison of forage utilization in the absence of the domestic herbivore (cattle), but not wild herbivores (deer and nilgai) for a companion study.

I installed each grazing exclosure in areas dominated by herbaceous vegetation representative of open grasslands where large herbivores would graze. The center of each grazing exclosure was the non-grazed sampling area. I marked the north corner of a paired outside sampling area with a t-post (Loft et al., 1987) at least 10 m from each grazing exclosure; this was the paired grazed sampling area. I attempted to reduce environmental heterogeneity between paired sampling areas by ensuring areas were: 1) in close proximity; 2) similar in percent cover of vegetation species and bare ground; and 3) as similar as possible in regard to proximity to shrubs, trees, and cacti.

While sampling areas predominately consisted of herbaceous vegetation, my objective was to estimate species richness; therefore woody plant seedlings and succulent propagules were included in estimates. I identified all plant species (forbs, grasses, sedges, sub-shrubs, succulent propagules, and woody seedlings) rooted within a 0.5 m × 0.5 m sampling frame within each of the grazing exclosures (non-grazed area) and 0.5 m from the t-post marking the paired grazed sampling area (grazed area). Within each grazing exclosure, the distance between the non-grazed sampled plot and the edge of exclosures was 0.5 m, which ensured vegetation was not disturbed by large ungulates. Birds may have roosted on grazing exclosures or t-post marking the grazed area and added nutrients via defecation (Bork and Werner, 1999) or small mammals may have pursued refuge within the grazing exclosure. I was unable to control for these inherent biases associated with this method.

In South Texas, most of the herbaceous forage production, representative of open grasslands, occurs in 2 periods, April to June and September to October (Fulbright and Ortega-S., 2013). Forbs germinate and produce most of their growth during late autumn through early spring while grasses produce most of their growth during summer through autumn (Fulbright and Ortega-S., 2013). Therefore, I examined species richness during autumn, when herbaceous forage was most abundant, and during spring.

For autumn sampling, grazing exclosures were in place for 8–12 months on each study site before sampling occurred. During November–December 2012 and September–October 2013 and 2014, all species were identified and herbaceous forage standing crop (forbs and grasses) was clipped at ground level within a 0.5 m × 0.5 m sampling frame placed in the center of each grazing exclosure. Herbaceous vegetation was also clipped in a 0.5 m × 0.5 m sampling frame placed 0.5 m from the t-post marking the paired grazed area. Only herbaceous forages were examined for standing crop because this study was conducted in conjunction with a companion study on utilization of herbaceous plants. Herbaceous forage samples were dried at 45°C until they reached a constant mass, then weighed to the nearest 0.1 g. After sampling was completed each autumn, grazing exclosures were moved 10 m in a randomly assigned cardinal direction (formerly sampled locations were avoided) and a new paired grazed area was selected and marked.

For spring sampling, grazing exclosures were in place for 5–6 months on each study site before sampling occurred. During March–April 2013 and 2014 and April–May 2015, all plant species were identified within a 0.5 m × 0.5 m sampling frame placed in the center of each grazing exclosure. Grazing exclosures remained in place after spring identification of vegetation species and the same location was re-sampled the following autumn. Therefore, I could not estimate herbaceous forage standing crop or estimate herbivore utilization during spring because destructive sampling would have interfered with the autumn sampling. I examined the relationship between potential plant species richness (e.g., within the grazing exclosures, thus protected for 5–6 months from large herbivores) during spring (e.g., peak growing season of forbs) and utilization of herbaceous vegetation by herbivores during autumn (e.g., previous growing season when both grasses and forbs are in peak growth). Because sampling locations were re-randomized after every autumn sampling period, the herbivore utilization of herbaceous vegetation the previous autumn calculated for each spring sampling location was within 30 m of the actual sampling location during spring (e.g., grazing exclosure and paired grazed area).

Statistical analyses

I compared competing models to examine the relationships between herbivore utilization, environmental variables, and standing crop of herbaceous vegetation with the difference in plant species richness between the grazed and non-grazed areas within each paired sampling location (e.g., grazed area and paired non-grazed area within grazing exclosure) during autumn (Table 3.1). In addition, I compared competing models to examine the relationships among herbivore utilization 5–6 months before sampling (e.g., autumn utilization of forages) and environmental variables with potential plant species richness within grazing exclosures (e.g., protected from grazing) during spring (Table 3.1). Because the species richness-herbivore relationship could be

Table 3.1. Proposed models to investigate competing theories regarding hypothesized factors influencing vegetation species richness 0.25 m^{-2} during peak growing seasons in South Texas, 2012–2015. During autumn, I employed a paired experimental design to compare the difference in species richness in a grazed area versus non-grazed area as it related to environmental factors (e.g., rainfall, temperature, soil texture defined by percentage of sand in soil), potential standing crop of herbaceous vegetation (biomass; determined from non-grazed area), and herbivore utilization at each sampling location. During spring, I determined if previous peak growing season's utilization of herbaceous forage influenced potential species richness (determined from non-grazed area) the following growing season.

Season		Proposed models
Autumn	1)	Utilization
	2)	Utilization + $(\text{utilization})^2$
	3)	Biomass
	4)	Seasonal rainfall + temperature + percent sand
	5)	Biomass + seasonal rainfall + temperature + percent sand
	6)	Utilization + seasonal rainfall + temperature + percent sand
	7)	Utilization + $(\text{utilization})^2$ + seasonal rainfall + temperature + percent sand
	8)	Utilization + biomass + seasonal rainfall + temperature + percent sand
	9)	Utilization + $(\text{utilization})^2$ + biomass + seasonal rainfall + temperature + percent sand
Spring	1)	Previous season utilization
	2)	Previous season utilization + $(\text{previous season utilization})^2$
	3)	Seasonal rainfall + temperature + percent sand
	4)	Previous season utilization + seasonal rainfall + temperature + percent sand
	5)	Previous season utilization + $(\text{previous season utilization})^2$ + seasonal rainfall + temperature + percent sand

monotypic or unimodal (Mackey and Currie, 2000, 2001), I examined models without and with the quadratic herbivore utilization variable.

Each randomly allocated paired sampling location (within exclosure and grazed area) was defined as the experimental unit. I considered pairs of exclosures and associated grazed area as experimental units because in heterogeneous environments, when variables collected at paired sampling locations are averaged across larger spatial scales, it disregards the spatial heterogeneity that naturally occurs in semiarid environments and the resulting model may not be representative of the landscape in which the study was conducted (Bork and Werner, 1999).

For autumn species richness data (2012–2014), I first calculated the difference in number of vegetation species per 0.25 m^2 in the grazed area (the treatment) minus the number of vegetation species per 0.25 m^2 in the non-grazed area (the control) for each paired sampling location. This calculation is analogous to a paired t-test. The null hypothesis of a paired t-test is H_o: $\mu_1 = \mu_2$ (e.g., μ_1 = species richness in the treatment and μ_2 = species richness in paired control) is statistically equivalent to the null hypothesis of my calculation for the difference in species richness, where H_o: $\mu_1 - \mu_2 = 0$. Hence, any value other than 0 for the difference in species richness (e.g., paired t-test null hypothesis would be rejected) would indicate a significant effect on species richness in the grazed compared to the non-grazed area. Because I calculated the difference in the treatment minus paired control, a positive value would indicate species richness increased in the grazed area, while a negative value would indicate species richness decreased in the grazed area. This calculation minimized spatial variability associated with vegetation communities across the landscape by computing a relative value that compared paired areas that had similar vegetation and were exposed to similar environmental conditions (e.g., comparing treatment to a paired control within close proximity; Bork and Werner, 1999).

Secondly, for each of my paired grazing exclosure locations, I calculated herbivore utilization of autumn herbaceous forage (HU) in a grazed area compared to its paired ungrazed area as:

$$HU\ (\%) = [\frac{(I - O)}{I}] * 100.$$

Where I is the standing crop of herbaceous forages (forbs and grasses) in the grazing exclosure (the control) and O is the standing crop of herbaceous forage in the grazed sampling area (the treatment). This relative utilization metric was used because my objective was to determine the impact of herbivore utilization of herbaceous forages (e.g., herbivory) on species richness (Bork and Werner, 1999). I calculated utilization for each sampling location, which minimized spatial variability associated with vegetation communities (Bork and Werner, 1999) and patchiness of herbivore utilization of forages across the landscape (Healy et al., 1997; Pringle and Landsberg, 2004; Tarhouni et al., 2010) by computing a relative value that compared paired areas with similar vegetation and were exposed to similar environmental conditions.

Herbivore utilization, when there is greater standing crop of herbaceous forages in the grazing exclosures compared to the paired grazed area, is bound between 0–100%. However, when standing crop of herbaceous vegetation is greater in the grazed area compared to the paired grazing exclosure, negative herbivore utilization values could be infinite. Negative utilization values occurred at one-quarter (*n* = 213) of the paired sampling locations during this study. Larger standing crop of herbaceous vegetation in the grazed area could have occurred by pure chance (Bork and Werner, 1999) or other factors such as compensatory growth in response to grazing (McNaughton, 1984, 1979; Oba et al., 2001), which has been documented for drought tolerant species under water stress conditions (Georgiadis et al., 1989; van Staalduinen and Anten, 2005). Therefore, negative utilization values could have biological meaning. I scaled negative utilization values so they were bound between -100–0% and retained these negative values in my regression models.

Retaining the full suite of utilization values applies more biological meaning to a relative calculation by including the entire gradient of vegetation comparisons which were present at paired sampling locations across the semiarid landscape. For example: 1) negative herbivore utilization values are representative of more herbaceous forage in the grazed area compared to its paired non-grazed area (e.g., hypothesized species richness would be lower in the grazed area relative to non-grazed area due to increased competition among vegetation species; Oba et al., 2001); 2) 0% herbivore utilization is representative of equal standing crop of herbaceous forages in the paired areas (e.g., where there should be no difference in species richness for paired vegetation sampling areas); and 3) positive herbivore utilization is representative of less herbaceous forage in the grazed area compared to its paired non-grazed area (e.g., hypothesized species richness may increase or decrease in the grazed area as forages are consumed).

Inclusion of negative values is: 1) more representative of heterogeneity associated with vegetation communities in semiarid arid systems; 2) does not bias utilization estimates (e.g., overestimating degree of herbivory) by zeroing out data; and 3) does not bias the statistical analysis employed to investigate the relationship among paired samples because it is analogous to a directionally-neutral test (e.g., two-tailed test examining normal distribution of population), whereas beginning at 0% utilization (e.g., removing all negative values from the data set) examines only a portion of the population, such as when employing a one-tailed statistical test (Bork and Werner, 1999). The inclusion of the negative utilization values and the use of relative calculations (e.g., both percent utilization and dependent variable used in my models) provided a more robust, yet conservative analysis, to determine the impact of large herbivore utilization on species richness (Bork and Werner, 1999).

Thirdly, I wanted to determine the model (see Table 3.1, pg. 52) that best explained species richness during autumn across the semiarid landscape. The dependent variable in all models was the difference in species richness between the grazed plots and exclosures, which allowed me to maintain my paired study design by analyzing the condensed paired t-test (one response variable representing the difference between pairs) in each regression model. Environmental variables included in models are primary factors influencing vegetation (Fulbright et al., 2008; Georgiadis et al., 1989; Krausman et al., 2009; Vavra, 2005; Walker and Wilson, 2002); I included 1) percent sand (continuous variable representative of soil texture) at each paired sampling location (USDA-NRCS, 2011a, 2011b), 2) autumn (August–September) rainfall received (obtained from weather stations located within each study site on Buena Vista, East El Sauz, and Santa Rosa and within 4.5–9.5 km of study sites on San Antonio Viejo ranch; Texas A&M AgriLife Research and Extension Center, 2015), and 3) a linear combination variable, determined from principle components analysis using Proc Princomp in SAS (version 9.3, SAS Institute, Cary, NC, USA), of temperature (daily minimum and maximum temperature averaged across August–September and average daily temperature during August–September; obtained from aforementioned weather stations; Table 3.2). The 3 individual temperature variables were collinearly related, thus instead, a linear combination variable (retained 78% of variation of 3 temperature variables) was included in each model so not to bias model results (Aguilera et al., 2006).

There was no multicollinearity among predictor variables included in models (condition index < 22.7; Haque et al., 2002). Model selection was determined using Akaike Information

Table 3.2. Mean daily temperature values (maximum, minimum, and daily average) and total rainfall received (obtained from weather station on ranch closest to each study site) during August–September, and percent sand in soil texture and potential standing crop of herbaceous forages (biomass; forbs and grasses within each 1.5 m × 1.5 m grazing exclosure) averaged across each sampling location (1.5 m × 1.5 m grazing exclosures; sample size = *n*) on 4 East Foundation ranches in South Texas, autumn 2012–2014.

		Temperature (°C)					Biomass
Site	*n*	Maximum	Minimum	Average	Rain (cm)	Sand (%)	(g 0.25 m^{-2})
2012							
Buena Vista	45	36.6	22.6	28.8	5.3	87.6	8.5
East El Sauz	45	33.1	23.0	27.9	8.1	86.0	35.3
Santa Rosa	48	36.1	22.7	28.3	10.7	85.0	15.5
San Antonio Viejo site 1	37	36.1	22.4	28.4	4.3	82.7	22.4
[1]SAV site 1 cattle exclosure	10	36.1	22.4	28.4	4.3	91.1	41.9
San Antonio Viejo site 2	37	36.1	22.4	28.4	4.3	80.1	15.7
[1]SAV site 2 cattle exclosure	9	36.1	22.4	28.4	4.3	79.3	17.9
San Antonio Viejo site 3	31	36.4	22.3	28.7	5.3	53.6	31.2
[1]SAV site 3 cattle exclosure	10	36.4	22.3	28.7	5.3	58.0	30.3
2013							
Buena Vista	50	34.7	22.7	27.8	0.3	87.6	29.0
East El Sauz	50	32.4	23.4	27.6	17.8	83.2	54.0
Santa Rosa	50	34.4	23.0	27.7	21.8	84.6	41.4
San Antonio Viejo site 1	40	34.3	22.7	27.5	17.0	82.3	12.1
[1]SAV site 1 cattle exclosure	10	34.3	22.7	27.5	17.0	91.1	35.8
San Antonio Viejo site 2	40	34.3	22.7	27.5	17.0	79.3	14.1
[1]SAV site 2 cattle exclosure	10	34.3	22.7	27.5	17.0	77.2	17.1
San Antonio Viejo site 3	35	34.9	22.2	27.6	16.8	53.3	30.3
[1]SAV site 3 cattle exclosure	10	34.9	22.2	27.6	16.8	58.0	19.9

[1] San Antonio Viejo (SAV).

Table 3.2. Continued.

Site	*n*	Temperature (°C) Maximum	Minimum	Average	Rain (cm)	Sand (%)	Biomass (g 0.25 m^{-2})
2014							
Buena Vista	50	34.6	23.0	27.8	4.1	87.6	40.9
East El Sauz	45	32.4	23.5	27.7	30.5	86.8	62.2
Santa Rosa	50	34.2	23.1	27.6	24.4	84.6	69.7
San Antonio Viejo site 1	40	34.3	22.8	27.6	10.7	82.3	38.5
[1]SAV site 1 cattle exclosure	10	34.3	22.8	27.6	10.7	91.1	61.6
San Antonio Viejo site 2	40	34.3	22.8	27.6	10.7	79.3	22.3
[1]SAV site 2 cattle exclosure	10	34.3	22.8	27.6	10.7	77.2	17.5
San Antonio Viejo site 3	37	34.4	22.6	27.6	12.2	53.9	27.4
[1]SAV site 3 cattle exclosure	10	34.4	22.6	27.6	12.2	58.0	33.2

[1] San Antonio Viejo (SAV).

Criterion (AIC). The top model selected had the lowest AIC score and characterized the most supported, parsimonious model of the models compared (Burnham and Anderson, 2002). In addition, I report Akaike model weights, which denotes the relative probability of each model. I analyzed data with generalized linear models (Proc Genmod; SAS, version 9.3, SAS Institute, Cary, NC, USA) with a Poisson distribution. I adjusted the parameter covariance matrix and the likelihood function by the scale parameter to correct for over dispersion (Proc Genmod dscale option; SAS, 2016).

Finally, I wanted to determine which variable (e.g., herbivore utilization, standing crop of herbaceous forages, or environmental variables) included in the top model were most influential on the difference in species richness during autumn. Using Akaike weights, I calculated importance weights (sum of all of model weights in which the variable is included) for each variable included in the top model to provide an estimate of the relative importance of each variable in explaining the difference in species richness (Dzialak et al., 2013).

For spring species richness data (2013–2015), the dependent variable for each model was the number of vegetation species per 0.25 m^2 in the non-grazed area (e.g., within center of each 1.5 m × 1.5 m grazing exclosure). I wanted to determine the model (see Table 3.1, pg. 52) that best explained potential species richness (e.g., protected from grazing for 5–6 months) during spring across the semiarid landscape. Environmental variables included in models were obtained as previously described, with exception of the weather variables. Rainfall and temperature variables included in models were assessed for November–February, prior to each spring sampling period (Table 3.3). The linear combination of the spring temperature variables included in the models retained 95% of the variation of the 3 individual spring temperature variables. The autumn herbivore utilization value for each sampling location included in the models was

Table 3.3. Mean daily temperature values (maximum, minimum, and daily average) and total rainfall received (obtained from weather station on ranch closest to each study site) during November–February, and percent sand in soil texture averaged across each sampling location (1.5 m × 1.5 m grazing exclosures; sample size = *n*) on 4 East Foundation ranches in South Texas, spring 2013–2015.

		Temperature (°C)				
Site	*n*	Maximum	Minimum	Average	Rain (cm)	Sand (%)
2013						
Buena Vista	45	24.2	11.6	17.6	5.8	87.6
East El Sauz	45	24.0	12.7	18.3	4.8	82.9
Santa Rosa	48	24.6	11.7	17.8	2.8	85.0
San Antonio Viejo site 1	37	23.7	12.2	17.4	4.1	82.7
[1]SAV site 1 cattle exclosure	10	23.7	12.2	17.4	4.1	91.1
San Antonio Viejo site 2	37	23.7	12.2	17.4	4.1	80.1
[1]SAV site 2 cattle exclosure	9	23.7	12.2	17.4	4.1	79.3
San Antonio Viejo site 3	31	24.2	11.5	17.6	4.6	53.6
[1]SAV site 3 cattle exclosure	10	24.2	11.5	17.6	4.6	58.0
2014						
Buena Vista	50	21.0	8.1	14.2	9.1	87.6
East El Sauz	50	20.7	9.2	14.8	18.5	82.3
Santa Rosa	50	21.2	8.3	14.3	3.6	84.6
San Antonio Viejo site 1	40	20.2	8.7	13.9	15.2	82.3
[1]SAV site 1 cattle exclosure	10	20.2	8.7	13.9	15.2	91.1
San Antonio Viejo site 2	40	20.2	8.7	13.9	15.2	79.3
[1]SAV site 2 cattle exclosure	10	20.2	8.7	13.9	15.2	77.2
San Antonio Viejo site 3	35	20.7	7.7	13.8	12.7	53.3
[1]SAV site 3 cattle exclosure	10	20.7	7.7	13.8	12.7	58.0

[1] San Antonio Viejo (SAV).

Table 3.3. Continued.

		Temperature (°C)				
Site	*n*	Maximum	Minimum	Average	Rain (cm)	Sand (%)
2015						
Buena Vista	50	20.4	8.6	14.0	13.2	87.6
East El Sauz	44	20.3	10.1	14.9	27.9	86.8
Santa Rosa	49	20.3	8.9	14.2	12.2	84.6
San Antonio Viejo site 1	40	19.6	9.3	13.8	17.3	82.3
[1]SAV site 1 cattle exclosure	10	19.6	9.3	13.8	17.3	91.1
San Antonio Viejo site 2	39	19.6	9.3	13.8	17.3	79.3
[1]SAV site 2 cattle exclosure	10	19.6	9.3	13.8	17.3	77.2
San Antonio Viejo site 3	37	20.2	8.6	13.8	14.7	53.9
[1]SAV site 3 cattle exclosure	10	20.2	8.6	13.8	14.7	58.0

[1] San Antonio Viejo (SAV).

calculated as described above. AIC was used to determine the top model (Burnham and Anderson, 2002), and calculated importance weights, previously described, for each variable included in the top model provided an estimate of the relative importance of each variable in explaining potential species richness during spring. There was no multicollinearity among predictor variables included in models (condition index < 22.2; Haque et al., 2002).

Results

During autumn 2012 – spring 2015, I identified 144 forb species (21 individuals could not be identified to species; Appendices B, C), 54 grass species (11 individuals could not be identified to species; Appendix D); 2 woody seedlings (*Prosopis glandulosa* and *Acacia minuata*), and 2 succulent propagules (*Opuntia engelmannii* and *O. leptocaulis*). The number of grass species identified during this study is typical of the South Texas region (60 species), but I identified fewer forb species than expected (up to 400 species) for this region (F. Smith, Director of South Texas Natives, personal communication).

Autumn

During autumn 2012–2014, standing crop of herbaceous forages in non-grazed area (e.g., representative of potential biomass at time of sampling) ranged from 0.1–440 g 0.25 m^{-2}, although most sampling locations (99.8%) were < 200 g 0.25 m^{-2} (*n* = 858). The difference in plant species richness between grazed and non-grazed areas ranged from -9–8 species 0.25 m^{-2} (Table 3.4). Across the study region during 2012–2014, mean (± 1 SE) utilization of herbaceous vegetation by large ungulates was 42.0% ± 1.2%. (range -100–100%; *n* = 858; Table 3.4).

Models that best represented the difference in plant species richness between grazed and non-grazed plots across the South Texas landscape included environmental variables (seasonal rainfall, temperature, and percentage of sand in soil), standing crop of herbaceous vegetation in non-grazed area (site productivity), and utilization of herbaceous vegetation by large herbivores (Table 3.5). Importance weights calculated for variables in the top model determined herbivore utilization of herbaceous vegetation (0.99) was 1.11 times more influential in shaping the difference in species richness than environmental variables (0.90) and 1.16 times more influential than site productivity (0.86). The difference in species richness was negatively related to increasing herbivore utilization and percentage of sand in the soil, but positively related to site productivity, rainfall, and temperature (Table 3.5).

Response of plant species richness to herbivore utilization was influenced by site productivity (based on standing crop of herbaceous vegetation in exclosures). When standing crop was 200 g $0.25m^{-2}$ (maximum value most representative of sampling locations), species richness in the grazed relative to the non-grazed area increased (i.e. difference in species richness > 0) with increasing herbivore utilization of herbaceous forages until utilization of forages was > 90%, at which point herbivory had no effect (e.g., difference in species richness = 0) on species richness; the difference in species richness ranged from 3–0 species 0.25 m^{-2} along the herbivore utilization gradient (-100–100%; Fig. 3.1).

Differences in plant species richness between grazed and non-grazed areas increased with increasing vegetation standing crop. After accounting for the effects of other variables in the model, for every 10 g 0.25 m^{-2} increase in standing crop of herbaceous vegetation, there was an additional 0.1 species 0.25 m^{-2} in the grazed compared to the non-grazed area (Table 3.6). When pairs of non-grazed and grazed plots occurred in areas of sparse vegetation, differences in species richness were smaller. For example, below 33 g 0.25 m^{-2} (the mean standing crop across study region), the difference in species richness was never more than 1, and large herbivore utilization of vegetation generally reduced (e.g., difference in species richness < 0) species richness in grazed compared to non-grazed areas.

While percentage of sand in the soil was also significant in the top model, the difference in plant species richness at the lowest (22%) and highest (92%) values of percentage of sand in the soil were similar along the herbivore utilization gradient (e.g., -100–100% utilization) at mean standing crop of herbaceous vegetation; the difference in species richness decreased from 2 to -1 and decreased from 1 to -2 at -100% to 100% utilization when percentage of sand in the soil was 22% and 92%, respectively (Table 3.6). A competing model was identified (ΔAIC of 0.363), which included the quadratic herbivore utilization parameter (e.g., unimodal shape); yet it had little influence on the relationship (e.g., not statistically significant at $\alpha = 0.05$; Table 3.6).

Table 3.4. Mean (± 1 SE) species richness 0.25 m^{-2} within the non-grazed (1.5 m × 1.5 m grazing exclosures) and paired grazed areas and mean (± 1 SE) utilization (%) of herbaceous vegetation, relative calculation for each paired non-grazed and grazed sampling location, by large herbivores for each 2 500 ha study site and each 65–152 ha cattle grazing exclosure site (cattle were excluded, but not deer and nilgai) on San Antonio Viejo ranch (SAV site # cattle exclosure), on 4 East Foundation ranches in South Texas, autumn 2012–2014. Species richness and percent utilization were averaged across sampling locations (*n*; paired non-grazed area within the 1.5 m × 1.5 m grazing exclosure and grazed area) for each site and year.

		Species richness 0.25 m^{-2}		
Site	*n*	Non-grazed	Grazed	Utilization
2012				
Buena Vista	45	5.4 ± 0.4	3.9 ± 0.4	45.6 ± 5.4
East El Sauz	45	5.0 ± 0.4	4.1 ± 0.3	57.6 ± 5.8
Santa Rosa	48	3.3 ± 0.2	1.6 ± 0.2	68.3 ± 4.9
San Antonio Viejo site 1	37	5.7 ± 0.4	3.7 ± 0.3	58.9 ± 5.7
SAV site 1 cattle exclosure	10	5.7 ± 0.5	6.7 ± 0.4	26.2 ± 10.3

Table 3.4. Continued.

		Species richness 0.25 m^{-2}		
Site	*n*	Non-grazed	Grazed	Utilization
2012				
San Antonio Viejo site 2	37	5.0 ± 0.5	3.0 ± 0.4	32.7 ± 4.8
SAV site 2 cattle exclosure	9	6.2 ± 0.8	4.9 ± 0.8	36.0 ± 12.9
San Antonio Viejo site 3	31	1.3 ± 0.2	0.6 ± 0.1	81.6 ± 5.0
SAV site 3 cattle exclosure	10	1.7 ± 0.3	1.2 ± 0.3	31.4 ± 14.5
2013				
Buena Vista	50	6.2 ± 0.4	5.4 ± 0.5	33.9 ± 4.8
East El Sauz	50	6.3 ± 0.5	5.0 ± 0.4	41.8 ± 4.5
Santa Rosa	50	5.1 ± 0.3	4.3 ± 0.3	40.0 ± 4.7
San Antonio Viejo site 1	40	6.0 ± 0.4	5.1 ± 0.4	35.3 ± 5.4
SAV site 1 cattle exclosure	10	8.6 ± 0.6	8.4 ± 0.7	33.4 ± 10.2
San Antonio Viejo site 2	40	8.6 ± 0.5	8.0 ± 0.4	23.2 ± 5.5
SAV site 2 cattle exclosure	10	10.7 ± 0.8	8.4 ± 1.0	38.6 ± 7.4
San Antonio Viejo site 3	35	2.2 ± 0.3	1.9 ± 0.3	49.6 ± 6.6
SAV site 3 cattle exclosure	10	4.9 ± 1.0	4.6 ± 0.9	42.8 ± 10.3
2014				
Buena Vista	50	7.6 ± 0.4	6.7 ± 0.4	25.3 ± 4.2
East El Sauz	45	6.6 ± 0.4	5.7 ± 0.4	49.0 ± 4.7
Santa Rosa	50	4.9 ± 0.4	4.8 ± 0.4	34.1 ± 4.6
San Antonio Viejo site 1	40	7.4 ± 0.4	7.6 ± 0.5	16.8 ± 3.3
SAV site 1 cattle exclosure	10	7.6 ± 0.6	7.2 ± 0.6	26.7 ± 8.2
San Antonio Viejo site 2	40	7.5 ± 0.5	6.2 ± 0.4	32.7 ± 4.8
SAV site 2 cattle exclosure	10	11.1 ± 0.5	9.9 ± 0.8	26.8 ± 8.7
San Antonio Viejo site 3	37	4.0 ± 0.5	3.6 ± 0.4	39.9 ± 6.3
SAV site 3 cattle exclosure	10	2.1 ± 0.7	2.0 ± 0.3	11.8 ± 5.5

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Table 3.5. Models and fit statistics for the difference in plant species richness 0.25 m^{-2} (grazed versus non-grazed area) on 4 East Foundation ranches in South Texas, autumn 2012─2014. Models are listed in order from the top model to the lowest ranking model (n = 858).

		[1]Model fit statistics		
	Model	[2]β[2]	ΔAIC	w_i
1)	Utilization + biomass + seasonal rainfall + temperature + percent sand	7	0.000	0.473
2)	Utilization + (utilization)^2 + biomass + seasonal rainfall + temperature + percent sand	8	0.363	0.393
3)	Utilization + (utilization)^2	4	4.303	0.055
4)	Utilization	3	4.859	0.042
5)	Utilization + (utilization)^2 + seasonal rainfall + temperature + percent sand	7	6.221	0.021
6)	Utilization + seasonal rainfall + temperature + percent sand	6	6.563	0.018
7)	Biomass	3	21.004	< 0.001
8)	Biomass + seasonal rainfall + temperature + percent sand	6	22.958	< 0.001
9)	Seasonal rainfall + temperature + percent sand	5	24.839	< 0.001

[1] Number of parameters (β), change in Akaike's Information Criterion score from the top model (ΔAIC), and Akaike model weights (w_i).

[2] The dscale option was needed to correct for over dispersion in the generalized linear model (Proc Genmod in SAS), thus an extra parameter (scale parameter) was estimated in all models and is reflected in the number of parameters (β) estimated for each model.

Table 3.6. Top model(s) parameter estimates (*β*) and 95% confidence intervals (CI) about parameter estimates, chosen based on AIC (see Table 3.5, pg. 63; Fig. 3.1), for the difference in plant species richness 0.25 m^{-2} (grazed versus non-grazed area) on 4 East Foundation ranches in South Texas, autumn 2012–2014 (*n* = 858). Two models were statistically equivalent (ΔAIC of 0.363).

			95 % CI			
[1]Parameter	*β* estimate		Lower		Upper	
	Top	Second	Top	Second	Top	Second
[2]Intercept	2.3270	2.3285	2.2146	2.2162	2.4394	2.4409
Utilization	-0.0016	-0.0007	-0.0022	-0.0020	-0.0011	0.0006
(Utilization)^2	—	< -0.0001	—	< -0.0001	—	> 0.0001
Biomass	0.0010	0.0010	0.0005	0.0004	0.0016	0.0016
Seasonal rainfall	0.0010	0.0010	-0.0021	-0.0021	0.0041	0.0041
Temperature	0.0006	0.0020	-0.0162	-0.0149	0.0174	0.0189
Percent Sand	-0.0013	-0.0013	-0.0025	-0.0025	-0.0001	-0.0001

[1] Generalized linear models were used and data were analyzed using log link function; all *β* estimates and 95% CI (wald 95% confidence limits) reported are on log scale. Therefore any parameter estimate with 95% CI that crosses 0 is not statistically significant at $\alpha = 0.05$. The estimated scale parameter (used to correct for over dispersion) is not included in this table (e.g., it does not affect parameter estimates).

[2] Intercept values reported still reflect data transformation; I added 10 to dependent variable so values would be positive and I could analyze data using a generalized linear model with Poisson distribution; thus correct value of the intercept (e.g., reflect data collected) would be calculated as [exp^(intercept) – 10].

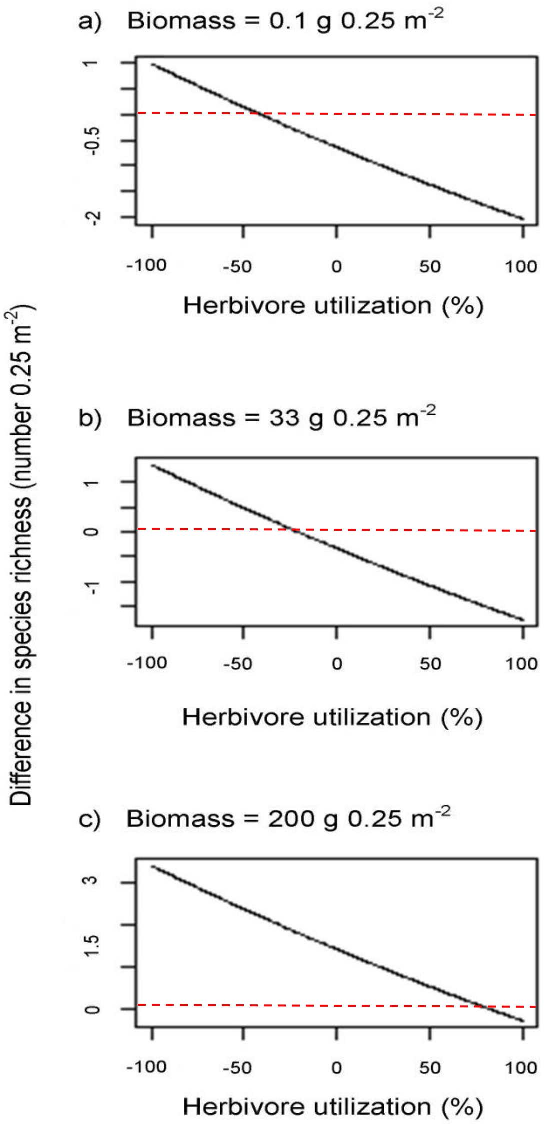

Figure 3.1.Relationship of the difference in plant species richness 0.25 m^{-2} (grazed minus non-grazed area) on 4 East Foundation ranches in South Texas, autumn 2012─2014, with the herbivore (herbivore utilization) and potential standing crop of herbaceous forages (biomass; forbs and grasses within each 1.5 m × 1.5 m grazing exclosures) at the minimum values (a), mean values (b) and maximum values (c; *n* = 858). If the difference in species richness is: 1) less than 0, then large herbivores decreased species richness; 2) equal to 0 (red-dashed line), then large herbivores had no effect on species richness; and 3) greater than 0, then large herbivores increased species richness in grazed relative to non-grazed areas.

Spring season

During spring 2013–2015, potential plant species richness (e.g., 1.5 m × 1.5 m areas where large herbivores had been excluded for 5–6 months) during spring ranged from 0–22 species 0.25 m^{-2} ($n = 856$; Table 3.7).

Models that best represented potential plant species richness during spring across the South Texas landscape included environmental variables (e.g., seasonal rainfall, temperature, percentage of sand in soil) and the herbivore (utilization of previous peak season's herbaceous forage) as a unimodal relationship (e.g., included quadratic herbivore utilization variable; Table 3.8). Importance weights calculated for variables in the top model determined environmental variables (1.00) were slightly more influential in shaping potential species richness than herbivore utilization of herbaceous vegetation (0.99). Potential species richness was positively related to seasonal rainfall and percentage of sand in the soil and negatively related to increasing temperatures (Table 3.9).

Potential plant species richness during spring displayed a hump-back relationship with herbivore utilization of the previous autumn vegetation (Table 3.9; Fig. 3.2); potential species richness 0.25 m^{-2} increased with increasing utilization, peaked at 20% utilization of autumn herbaceous forage, and then declined with increasing utilization after accounting for environmental variables. At peak potential of species richness (e.g., when herbivore utilization was 20%) during spring, while accounting for other variables in the model, there was: 1) an increase of 4.2 species 0.25 m^{-2} as percentage of sand in the soil increased from 22% to 92% (e.g., mostly annual forbs adapted to sandy soils; Fig. 3.2); 2) an increase of 2.3 species 0.25 m^{-2} as seasonal rainfall increased from 2.8 cm to 28 cm; and 3) a decrease of 3.6 species 0.25 m^{-2} as temperature increased from the lowest (maximum 20°C, minimum 8°C, average 14°C) to the highest (maximum 25°C, minimum 13°C, average 18°C) temperature values (e.g., linear combination of all three temperature variables; temperature relationship is not displayed; Table 3.9).

Table 3.7. Mean (± 1 SE) potential plant species richness 0.25m^{-2} (e.g., non-grazed area where large herbivores were excluded for 5–6 months) during spring (e.g., peak growing season of forbs) following utilization of autumn herbaceous vegetation (e.g., peak growing season of grasses and forbs) for each 2 500 ha study site and each 65–152 ha cattle grazing exclosure site (cattle were excluded, but not deer and nilgai) on San Antonio Viejo ranch (SAV site # cattle exclosure), on 4 East Foundation ranches in South Texas, 2013–2015. Potential species richness was averaged across non-grazed (within 1.5 m × 1.5 m grazing exclosures) sampling locations (*n*) for each study site and year.

Site	*n*	Potential species richness 0.25 m^{-2}
2013		
Buena Vista	45	5.4 ± 0.3
East El Sauz	45	4.2 ± 0.3
Santa Rosa	48	3.5 ± 0.2
San Antonio Viejo site 1	37	4.1 ± 0.3
[1]SAV site 1 cattle exclosure	10	4.4 ± 0.5
San Antonio Viejo site 2	37	3.7 ± 0.3
[1]SAV site 2 cattle exclosure	9	3.7 ± 0.5
San Antonio Viejo site 3	31	1.0 ± 0.2
[1]SAV site 3 cattle exclosure	10	2.0 ± 0.4
2014		
Buena Vista	50	6.8 ± 0.4
East El Sauz	50	5.5 ± 0.4
Santa Rosa	50	5.2 ± 0.3
San Antonio Viejo site 1	40	8.1 ± 0.4
[1]SAV site 1 cattle exclosure	10	7.2 ± 0.3
San Antonio Viejo site 2	40	7.6 ± 0.4
[1]SAV site 2 cattle exclosure	10	9.9 ± 0.5
San Antonio Viejo site 3	35	3.4 ± 0.4
[1]SAV site 3 cattle exclosure	10	2.8 ± 0.4

Table 3.7. Continued.

Site	*n*	Potential species richness 0.25 m^{-2}
2015		
Buena Vista	50	10.6 ± 0.4
East El Sauz	44	7.4 ± 0.4
Santa Rosa	49	8.7 ± 0.5
San Antonio Viejo site 1	40	10.2 ± 0.4
[1]SAV site 1 cattle exclosure	10	7.9 ± 0.4
San Antonio Viejo site 2	39	10.2 ± 0.4
[1]SAV site 2 cattle exclosure	10	10.0 ± 0.9
San Antonio Viejo site 3	37	5.6 ± 0.5
[1]SAV site 3 cattle exclosure	10	2.9 ± 0.4

Table 3.8. Models and fit statistics for potential plant species richness 0.25 m^{-2} (e.g., non-grazed area where large herbivores were excluded for 5–6 months) during spring (e.g., peak growing season of forbs) following utilization of autumn herbaceous vegetation (e.g., peak growing season of grasses and forbs) on 4 East Foundation ranches in South Texas, 2013–2015. Models are listed in order from the top model to the lowest ranking model (n = 856).

	[2]Model	[1]Model fit statistics		
		β	ΔAIC	w_i
1)	Previous season utilization + (previous season utilization)^2 + seasonal rainfall + temperature + percent sand	7	0.000	0.938
2)	Previous season utilization + seasonal rainfall + temperature + percent sand	6	5.462	0.061
3)	Seasonal rainfall + temperature + percent sand	5	13.613	0.001
4)	Previous season utilization + (previous season utilization)^2	4	475.416	< 0.001
5)	Previous season utilization	3	535.275	< 0.001

[1] Number of parameters (β), change in Akaike's Information Criterion score from the top model (ΔAIC), and Akaike model weights (w_i).

[2] The dscale option was needed to correct for over dispersion in the generalized linear model (Proc Genmod in SAS), thus an extra parameter (scale parameter) was estimated in all models and is reflected in the number of parameters (β) estimated for each model.

Table 3.9. Top model parameter estimates (*β*) and 95% confidence intervals (CI) about parameter estimates, chosen based on AIC (see Table 3.8; pg. 72; Fig. 3.2), for potential plant species richness 0.25 m^{-2} (e.g., non-grazed area where large herbivores were excluded for 5–6 months) during spring (e.g., peak growing season of forbs) following utilization of autumn herbaceous vegetation (e.g., peak growing season of grasses and forbs) on 4 East Foundation ranches in South Texas, 2013–2015 (*n* = 856).

[1]Parameter	*β* estimate	95 % CI Lower	95 % CI Upper
Intercept	0.7256	0.5307	0.9204
Previous season utilization	0.0012	-0.0011	0.0036
(Previous season utilization)^2	< -0.0001	-0.0001	< -0.0001
Seasonal rainfall	0.0138	0.0082	0.0195
Temperature	-0.1394	-0.1664	-0.1125
Percent sand	0.0118	0.0096	0.0140

[1] Generalized linear models were used and data were analyzed using log link function; all *β* estimates and 95% CI (wald 95% confidence limits) reported are on log scale. Therefore any parameter estimate with 95% CI that crosses 0 is not statistically significant at $\alpha = 0.05$. The estimated scale parameter (used to correct for over dispersion) is not included in this table (e.g., it does not affect parameter estimates).

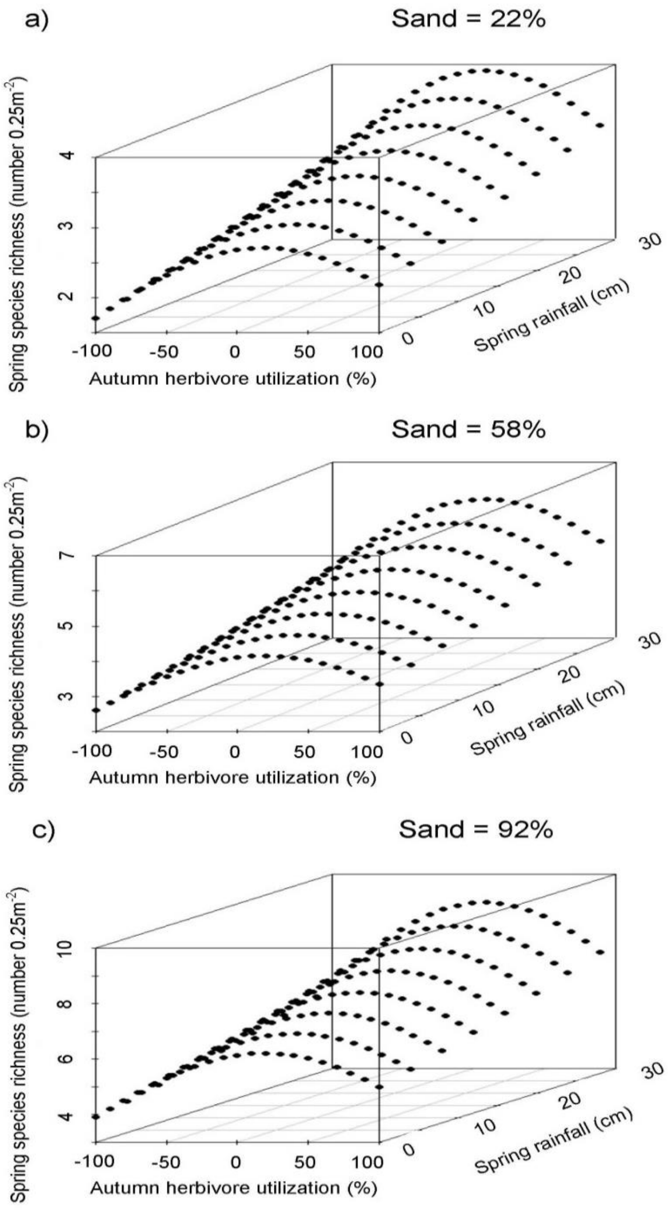

Figure 3.2. Potential species richness 0.25 m^{-2} (e.g., non-grazed area where large herbivores were excluded for 5–6 months) during spring as it related to herbivore (utilization of autumn herbaceous vegetation), seasonal rainfall, and minimum percentage of sand in soil (a), median percentage (b), and maximum percentage (c) on 4 East Foundation ranches in South Texas, 2013–2015 (*n* = 856). Potential species richness peaked when herbivore utilization was 20%, and increased with both increasing rainfall and percentage of sand in the soil.

Discussion

Large herbivores were either the most important driver or a similarly important driver as abiotic factors on plant species richness. I conducted this study in a semiarid environment where the average coefficient of variation (CV) in interannual rainfall was 34% during 2012–2015, but herbivores were not decoupled from vegetation dynamics as predicted by non-equilibrium dynamics. Multiple researchers have proposed when CV in interannual rainfall is > 33%, as it was during this study, herbivores would have little detectable influence on vegetation dynamics (e.g., non-equilibrium dynamics; Ellis and Swift, 1988; Von Wehrden et al., 2012) because abiotic factors primarily effect vegetation dynamics (Diaz et al., 2007; Walker and Wilson, 2002). While herbivores may not affect all aspects of vegetation dynamics (i.e., standing crop of vegetation) in semiarid environments, they do impact species richness. These findings support a hypothesis proposed by Aldo Leopold (1933); in semiarid systems, large herbivores will have little influence on standing crop of vegetation, but will impact species composition. However, herbivory by large herbivores was not the sole driver either; a combination of herbivory, site productivity, and abiotic factors influenced plant species richness.

My results did support the hypothesis that abiotic factors influence the species richness-herbivore relationship in semiarid environments. Site productivity (measured in this study as standing crop of herbaceous vegetation at the time of sampling) impacts the herbivore effect on species richness as reported by Bakker et al., 2006; Burns et al., 2009; Frank, 2005; and Oba et al., 2001. Yet the shape of the species richness-herbivore relationship (e.g., monotypic or unimodal) depended on if vegetation was or was not protected from grazing by large herbivores, not site productivity as previously hypothesized.

Postulates regarding the shape (e.g., unimodal or monotypic) of the species-richness relationship to disturbance (i.e., grazing by large herbivore) predict the relationship changes along a productivity gradient; monotypic (neutral to negative) in dry, low productive grasslands (0–300 g m^{-2}; e.g., Bakker et al., 2006) and unimodal in mesic, high productive grasslands (300–600 g m^{-2}; e.g., Bakker et al., 2006; Milchunas and Lauenroth, 1993; Milchunas et al., 1988; Oba et al., 2001; Olff and Ritchie, 1988). Our study region would be characterized as a low productive grassland (e.g., 92% of sampling locations, out of $n = 858$, standing crop of herbaceous vegetation was < 300 g m^{-2}). Yet, I found that both relationship patterns (e.g., monotypic and unimodal) occurred in a low productive grassland; there was a negative linear (monotypic) relationship between species richness and herbivore utilization when large herbivores had access to graze vegetation (e.g., during autumn) and displayed a hump-back (unimodal) relationship when vegetation was protected from large herbivore grazing (e.g., spring where herbivores were excluded from sampling areas 5–6 months).

This landscape scale study validates the need to exercise conservative management practices in highly stochastic, semiarid landscapes (e.g., Holechek et al., 2011). Projected impacts on plant species richness during autumn, based on top model from this study, predicts when site productivity is at least 400 g m^{-2} (e.g., 100 g 0.25 m^{-2}) and large herbivore utilization of autumn vegetation is conservative (20%), the herbivore impact on autumn species richness will be neutral (e.g., difference in species richness = 0), whether drought or non-drought conditions (Table 3.10). However, when site productivity is less than 400 g m^{-2}, large herbivores will decrease (e.g., difference in species richness < 0) autumn species richness in grazed compared to non-grazed areas; this result supports findings of others– grazing by large herbivores decreases species richness in low productive grasslands (Bakker et al., 2006).

However, Bakker et al. (2006) proposed a site productivity value of 300 g m^{-2} (e.g., 0.75 g 0.25 m^{-2}) as the dividing line between when grazing by large herbivores decreases species richness to when grazing by large herbivores has no effect on species richness. While, this landscape scale study determined a higher site productivity value, 400 g m^{-2} (e.g., 100 g 0.25 m^{-2}), as the dividing line between when grazing by large herbivores decreases species richness to when grazing by large herbivores has no effect on species richness in a semiarid environment. Furthermore, potential plant species richness during spring (e.g., herbivores were excluded from vegetation for 5–6 months) peaked when herbivore utilization of autumn herbaceous vegetation was also conservative (e.g., 20% utilization). In semiarid systems where herbivores migrate seasonally, conservative utilization of the previous peak season's vegetation maximizes species richness the following growing season. While the increased potential spring species richness found in this study was small, ranged 2–4 species 0.25 m^{-2}, it was similar to values (~ 4 species) reported in literature reviewed by Mackey and Currie (2000, 2001).

Conservative management practices are required in semiarid environments to ensure grazing by large herbivores, both domestic and wild, does not decrease species richness. Conserving and increasing species richness across rangelands not only enhances biodiversity (Archer and Smeins, 1991; Stohlgren et al., 1999) on lands that encompass one-third of the terrestrial ecosystem (Asner et al., 2004; Briske et al., 2015), but also benefits health and production of large herbivores (Wang et al., 2010) thereby positively impacting ecosystem goods and services they provide to millions of humans (Curtis, 2002; Sayre et al., 2013; Watkins et al., 2007).

Table 3.10. Projected impacts on autumn species richness in grazed compared to non-grazed areas (Difference in species richness) in a semiarid environment, with mostly sandy soils, during drought conditions (50% of expected seasonal rainfall received during August–September) and non-drought conditions based on varying site productivity (biomass; measured in this study as standing crop of herbaceous vegetation at the time of sampling), based on top model from this landscape scale study conducted on 4 East Foundation ranches in South Texas, autumn 2012–2014. When the difference in species richness is: 1) less than 0, then large herbivores will decrease species richness; and 2) equal to 0, then large herbivores will have no effect on species richness in grazed compared to non-grazed areas.

	Biomass (g 0.25 m^{-2})	Difference in species richness (species 0.25 m^{-2})
Drought	[*]22	-0.8
	[†]105	0.0
Non-Drought	[*]33	-0.6
	[†]100	0.0

[*] Average potential standing crop of herbaceous vegetation determined during this study during drought and non-drought conditions.

[†] Minimum potential standing crop of herbaceous vegetation required for herbivore impact on species richness to change from negative to neutral. Approximately 8% of paired sampling locations had standing crop > 100 g 0.25 m^{-2}.

CHAPTER IV

DIETARY NICHE PARTITIONING AMONG CATTLE, DEER, AND NILGAI USING STABLE ISOTOPES

Introduction

Investigation of diets of domestic and wildlife species and determination of the dietary niche space of these species have been a subject of pronounced importance in ecological, extension, and popular literature. Results of these studies can have profound management implications as an understanding of dietary niche partitioning provides insight into potential competition for forages between sympatric species (e.g., dietary niche partitioning reduces potential competition). For decades, ecologists have debated the constituents influencing the dietary niche space of an animal (Ditchkoff, 2000; Hanley, 1982; Hofmann, 1989; Shipley et al., 2009).

Dietary niche space occupied by an animal is a complex aggregate of factors including: 1) forages consumed; 2) forages available to consume; and 3) temporal and spatial scales investigated (Shipley et al., 2009). Evolutionary adaptations of species can dictate relationships of dietary niche space among species (Hanley, 1982; Hofmann, 1989). Larger bodied animals, for example, typically have longer retention time of forages, thus can obtain needed nutrition from lower quality forages compared to smaller bodied animals. For larger herbivores, dietary niche space along the dietary niche continuum ranges from browsers (consume <25% grasses) to grazers (consume >75% grasses), with intermediate foragers between the two extremes (Hofmann and Stewart, 1972). Although this idea was formalized >40 years ago, postulates regarding how and why herbivorous species are arranged in dietary niche space remain controversial.

Hanley (1982) proposed species should be classified along the dietary niche continuum based on body size and morphological characteristics of digestive anatomy. Hoffman (1989) recognized there were inconsistences in body size along the dietary niche continuum and introduced the Ruminant Diversification hypothesis, proposing the primary determinate of dietary niche classification should be based on morphological characteristics of digestive anatomy. Experimental validation of these hypotheses is lacking (Ditchkoff, 2000) and ruminants are typically arranged along the dietary niche continuum based on postulates proposed from these hypotheses and diet investigation studies (Fulbright and Ortega-S., 2013).

Dietary niche classification established from past diet investigation methods (e.g., bite counts, microhistological, and rumen content analysis), may be inadequate for feeding guild classification because of biases associated with methods, including time constraint, observational, and digestibility biases (Ambrose and DeNiro, 1986). Stable isotope analysis of animal tissues determines assimilated diet over a certain time period, dependent on the turnover rate of each animal tissue, and lessens the potential for biases associated with past methods (Ambrose and DeNiro, 1986; Codron et al., 2011). Isotopes of an element have the same number of protons and electrons, but a different number of neutrons, and therefore differ in mass (Campbell and Reece, 2005). The heavier isotope of an element (e.g., has more neutrons) is relatively less abundant in the environment than the lighter isotope (Dawson et al., 2002). Stable isotope abundances of a sample (i.e., animal tissue) are reported as delta (δ) values which are calculated as $[1000 * (R_{sample} / R_{standard} - 1)]$ in parts per thousand (‰), where R_{sample} is the ratio of the heavier isotope to the lighter isotope of the sample and $R_{standard}$ is the ratio of the heavy to light isotope of a known standard (Dawson et al., 2002; Peterson and Fry, 1987). By definition, standards have arbitrarily been assigned a δ value of 0‰, hence when a sample has a positive δ signature, it contains more of the heavier isotope and a negative δ signature indicates the sample contains less of the heavier isotope, relative to the standard (Dawson et al., 2002). If forages consumed by ruminants have distinct isotope signatures, then stable isotope analysis of ruminant tissues can be used to detect differences in forage utilization (Gannes et al., 1998) and could be used to investigate the arrangement of ruminants along the dietary niche continuum.

In South Texas, forage classes have distinct $\delta^{13}C$ (carbon) and $\delta^{15}N$ (nitrogen) isotope signatures (Hines et al., unpublished data). Most grasses in South Texas use the C_4 photosynthetic pathway, whereas forbs and woody plants are predominately C_3 plants. C_4 plants assimilate more of the heavier carbon isotope (^{13}C) relative to C_3 plants during photosynthesis. Hence, the $\delta^{13}C$ signature of grasses in South Texas is more positive (average range -16.2 to -12.9 ‰) than the $\delta^{13}C$ signature of forbs and woody plants (average range -29.6 to -23.6 ‰; Hines et al., unpublished data). However, in South Texas, the $\delta^{13}C$ signature of succulents (average range -14.9 to -12.6 ‰) most commonly used by large herbivores as a food resource (*Opuntia engelmannii* and *O. leptocaulis*) were not distinguishable from grasses (Hines et al, unpublished data). Although, the $\delta^{15}N$ signature of succulents (average 9.6 ‰) distinguished succulents from grasses, forbs, and woody plants (average range 4.2–4.6 ‰). The $\delta^{13}C$ and $\delta^{15}N$ isotope signatures of ruminants' tissues provides an unbiased method to investigate dietary niche space of South Texas ruminants.

White-tailed deer (*Odocoileus virginianus*), nilgai (*Boselaphus tragocamelus*), and cattle (*Bos spp.*) have been classified along the dietary niche continuum as browsers (<10% grasses in diet), intermediate feeders (60–70% grasses), and grazers (80–90% grasses), respectively, based on morphological differences (body size and digestive anatomy) and past diet studies (Fig. 4.1; Fulbright and Ortega-S., 2013). My objective was to determine if diet composition of white-tailed deer, nilgai, and cattle followed the body size and rumino-reticulum to body weight ratio hypotheses, with deer being primarily browsers, cattle primarily grazers, and nilgai as intermediate feeders closer to grazers than browsers. Because these ruminants have been classified into distinct feeding guilds, I predicted there would be minimal overlap in dietary niches of sympatric populations of cattle, white-tailed deer, and nilgai.

Methods

Study site description

I selected six 2 500 ha study sites (10–134 km apart) located on 4 East Foundation ranches spanning the semiarid region from the Gulf Coast to western South Texas, USA (Fig. 2.2, pg. 23). There was one study site on each of the following ranches: 1) Buena Vista in Jim Hogg County (6 113 ha), 2) East El Sauz in Willacy County (10 984 ha), and 3) Santa Rosa in Kenedy County (7 544 ha). Three study sites were located on San Antonio Viejo, 60 034 ha, in Jim Hogg and Starr counties with a study site in the northern (site 1), central (site 2), and southern (site 3) portion of the ranch. The 2 500 ha study site within each ranch were chosen: 1) based on the center of the ranch (Buena Vista and Santa Rosa); 2) based on the center, southern portion of ranch (East El Sauz) to avoid active sand dunes and dense live oak mottes because these are not conductive to all large herbivores (e.g., domestic cattle) utilizing the area; and 3) in conjunction with another study based on the central location of 3 separate white-tailed deer captures (3 sites on San Antonio Viejo) that occurred the previous year.

Most study sites were located in the Coastal Sand Plain ecoregion. However, San Antonio Viejo site 3 was located in the Tamaulipan Thornscrub ecoregion. The Coastal Sand Plain ecoregion consists of mostly open grasslands with interspersed woody mottes, while the Tamaulipan Thornscrub ecoregion consists of thicker, thornscrub woodlands. Detailed

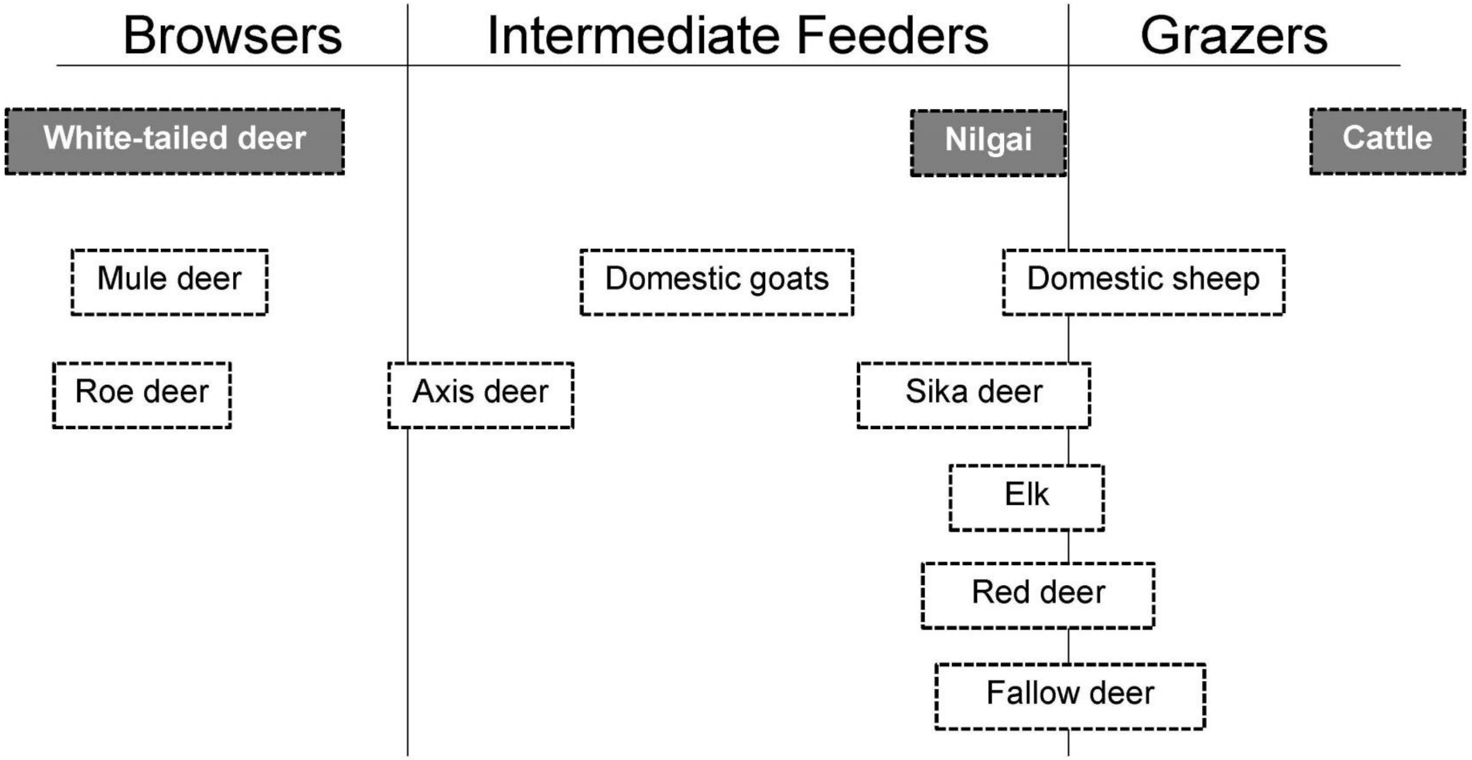

Figure 4.1. Dietary niche space of cattle, deer, and nilgai along the dietary niche continuum; classified based on morphological characteristics of digestive anatomy, body size, and in part, bite count and rumen content analysis research. Along the continuum, progressing from browsers (far left) to grazers (far right), the percentage of grasses in the diet increases. Vertical alignment of species indicates similar diet (e.g., compete for forages). Figure adapted, with permission, from Fulbright and Ortega-S. (2013).

descriptions of vegetation for the Coastal Sand Plain are described in Diamond and Fulbright (1990), Forman et al. (2009), Fulbright (2001), and Fulbright et al. (1990). Detailed descriptions of the Tamaulipan Thornscrub are in Fulbright (2001).

Cattle and deer were present on all six study sites, but distribution of nilgai is mostly constrained to the eastern region of South Texas. Nilgai were prevalent at Santa Rosa and East El Sauz, although there was a small population at San Antonio Viejo ranch. Across the study region during 2013–2015, population density estimates for cattle ranged from 13.3–21.9 cattle km^{-2} and white-tailed deer ranged from 8.2–13.3 deer km^{-2}. Density estimates for nilgai at Santa Rosa and East El Sauz ranged from 4.3–10.5 nilgai km^{-2}; no population density estimates for nilgai were available for San Antonio Viejo ranch because nilgai densities were too low for estimates to be made (Annala, 2015).

Stable isotope dietary niche

Diet composition of herbivores can vary with changes in available forage and among seasons (Armstrong, 1981; Drawe and Box, 1968; McMahan, 1964; Thill and Martin, 1989; Willms et al., 1980), and studies have shown diet composition of sympatric herbivores is most similar during winter, when forage is generally limiting. Thus, I investigated diet composition of large South Texas herbivores across multiple seasons (during peak growing seasons – when forage was near its maximum nutritional quality and digestibility, and during winter) and multiple years (2012–2015). Forbs are at peak growth during both spring and autumn. However, autumn is the only season in South Texas when both forbs and grasses are concurrently in peak growth (Fulbright and Ortega-S., 2013). The $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures of feces reflect herbivore diet consumed (Codron and Codron, 2009) within 2-weeks of eating a novel diet (e.g., analogous to consuming novel forage available during peak growing season; Sponheimer et al., 2003). During autumn and spring, at least 2-weeks after rain events when herbaceous vegetation was most abundant, I randomly collected fresh fecal samples (<2 days old) for cattle, deer, and nilgai (where present), across each 2 500 ha study site. Fecal samples were collected as a result of a chance-encounter by stopping at random locations when I saw a fecal deposit on the road or by searching for samples along visible animal trails. During a drought period from autumn 2012 through spring 2013, I collected fecal samples by the end of October (autumn season) and April (spring season). For winter, I ensured a rainfall event had not occurred within 2-weeks of sample collection to investigate stable isotope dietary niche for each ruminant species when herbaceous forage was most limiting. The goal was to collect 20 fresh fecal samples per species each season and year (Stewart et al., 2003). However, my sample size for each species (each site, season, year during this study) ranged from 11–20 because I only collected fresh fecal samples (e.g., those reflecting diets within a season) and I collected samples over a short time period (within 3-7 days across all sites during each season) to ensure samples were collected under similar environmental conditions. I opportunistically collected nilgai fecal samples at San Antonio Viejo ranch (n = 1–10), and included these nilgai samples in statistical analyses when $n \geq 6$ because the 95% stable isotope dietary niche confidence ellipse was comparable to when $n = 20$ (e.g., comparable to nilgai stable isotope dietary niches at Santa Rosa and East El Sauz).

Fecal samples were dried at 45 °C to a constant mass. Debris, vegetation, and insects externally attached to fecal samples (evidence of non-ingested material) were removed from samples. Fecal samples were homogenized into a powder using an oscillating mill (Retsch, Haan, Germany). Homogenized fecal samples were submitted to the Stable Isotopes for Biosphere Science Laboratory (Texas A&M University, College Station, Texas) for dual δ^{13}C and δ^{15}N stable isotope analysis (SIBS, 2016).

Statistical analysis

Analyses were conducted using fecal $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures. Changes in the δ isotope signature from the diet to feces is called fractionation ($\Delta_{feces\text{-}diet}$; Peterson and Fry, 1987; Dawson et al., 2002) and occurs because of chemical, physical, and biological processes that occur during digestion and assimilation of the diet (e.g., not all of the carbon and nitrogen in feces are derived from the diet, but some are from animal's body; Gannes et al., 1998). I was not able to correct the fecal isotope signature to reflect diet because $\delta^{15}N$ $\Delta_{feces\text{-}diet}$ rate for cattle was unknown. The analysis of the fecal isotope signature with multiple species (e.g., cattle, deer, and nilgai) and isotopes (e.g., isotopes of carbon and nitrogen) biases the analysis conducted in this study because the $\Delta_{feces\text{-}diet}$ varies depending on animal species, forages consumed (e.g., C_4 or C_3 diet), and isotope (Hines et al., unpublished data). However, the $\delta^{13}C$ $\Delta_{feces\text{-}diet}$ is < 3‰ for cattle and deer (Hines et al., unpublished data) and the $\delta^{15}N$ $\Delta_{tissue\text{-}diet}$ is typically < 5‰ for herbivores (Darr and Hewitt, 2008; Gannes et al., 1998). The $\delta^{13}C$ and $\delta^{15}N$ $\Delta_{feces\text{-}diet}$ values are very small, resulting in a slight shift in the $\delta^{13}C$ and $\delta^{15}N$ isotope signatures when corrected to reflect diet. Hence, the correction applied to fecal $\delta^{13}C$ and $\delta^{15}N$ isotope signatures to reflect diet consumed would not result in a substantial shift in the stable isotope dietary niche space of cattle, deer, and nilgai.

I analyzed fecal stable isotope dietary niches of cattle, deer, and nilgai using multivariate analysis of variance (MANOVA) blocked by study site, season, and year in SAS (version 9.3, SAS Institute, Cary, NC, USA). MANOVA is a multivariate f-test that examines variation within and between (e.g., definition of dietary niche width) the linear combination of the $\delta^{13}C$ and $\delta^{15}N$ isotope signatures of each species (e.g., the independent variable). Site, season, and year interacted ($P < 0.001$), thus I analyzed stable isotope dietary niches for each species separately for each study site, every season and year. If there were no statistical differences ($P > 0.05$), then the stable isotope dietary niche of species overlapped. To determine species differences for study sites with >2 species (e.g., cattle, deer, and nilgai), I conducted pairwise comparisons using the Tukey-Kramer test on the linear combination of the $\delta^{13}C$ and $\delta^{15}N$ fecal isotope signatures (retained >90% of variation of the two isotope variables) for each study site. Because MANOVA assumes multivariate normality, results were verified using a multivariate permutation-based MANOVA (PerMANOVA) with both Euclidean (similar assumptions to MANOVA) and Bray-Curtis (relaxed assumptions compared to MANOVA) distance measures in PC-ORD (version 6, MjM Software Design, Gleneden Beach, OR, USA; Peck, 2010).

Dietary niche space placement along the dietary niche continuum

The seasonal mean fecal carbon isotope signature, across sites and years, was corrected to reflect the diet for each species. This correction produces comparable $\delta^{13}C$ signatures among species (e.g., reflects diet consumed) and was used to determine where species were placed along the dietary niche continuum because the $\delta^{13}C$ signature can be used to determine the percentage of C_4 (grasses) plants consumed by the animal in South Texas (e.g., most grasses utilize the C4 photosynthetic pathway, whereas most forbs/woody plants are C_3 plants). For cattle and deer, the $\Delta_{\text{feces-diet}}$ was determined from a feeding trial I conducted during summer 2013 (Hines et al., unpublished data) and it accounted for digestibility of forages consumed (Codron et al., 2011). Because cattle have been classified as grazers and deer as browsers, I corrected the mean seasonal fecal isotope signature using the fractionation rate for cattle consuming 100% C_4 diet ($\Delta_{\text{feces-diet}}$ 2.66 ‰; e.g., representative of grazer diet in South Texas) and the fractionation rate for deer consuming 100% C_3 diet ($\Delta_{\text{feces-diet}}$ 0.36 ‰; e.g., representative of browser diet in South Texas). I did not determine the feces-diet fractionation rate for nilgai. However because nilgai have been classified as intermediate feeders, I assumed their feces-diet fractionation rate would be between deer on 100% C_3 diet and cattle on 100% C_4 diet. I used equations set forth by Codron and Codron (2009) to determine the percentage of C_4 forages (e.g., grasses) in each species mean seasonal diet.

Results

Unless the P-value < 0.0001 for species comparisons, the 95% fecal stable isotope confidence ellipses between species were not completely separate and several individuals from both species had similar diets. Therefore, dietary niche space overlap among species was defined based on the following categories: 1) complete separation of fecal stable isotope dietary niches ($P < 0.0001$); 2) slight overlap of fecal stable isotope dietary niche with several individuals having similar diets ($0.0001 < P < 0.05$); and 3) overlap of fecal stable isotope dietary niches ($P > 0.05$).

Autumn

During autumn 2012–2014, fecal stable isotope dietary niches of: 1) cattle and nilgai were separate ($P < 0.0001$) in 100% of comparisons, 2) cattle and deer were separate ($P < 0.0001$) in 90% of comparisons, individuals of cattle and deer had similar diets ($P = 0.0006$) in 5% of comparisons, and overlapped ($P = 0.0525$) in 5% of comparisons, and 3) individuals of deer and nilgai had similar diets ($P \leq 0.0231$) in 43% of comparisons and deer and nilgai overlapped ($P \geq 0.2845$) in 57% of comparisons (Table 4.1; Fig. 4.2).

Spring

During spring 2013–2015, fecal stable isotope dietary niches of: 1) cattle and nilgai were separate ($P < 0.0001$) in 86% of comparisons and individuals of cattle and nilgai had similar diets ($P = 0.0007$) in 14% of comparisons; 2) cattle and deer were separate ($P < 0.0001$) in 100% of comparisons; and 3) deer and nilgai were separate ($P < 0.0001$) in 43% of comparisons, individuals of deer and nilgai had similar diets ($P \leq 0.0436$) in 43% of comparisons, and overlapped ($P = 0.5655$) in 14% of comparisons (Table 4.1; Fig. 4.3).

Winter

During winter 2013–2015, fecal stable isotope dietary niches of: 1) cattle and nilgai were separate ($P < 0.0001$) for 90% of comparisons and individuals of cattle and nilgai had similar diets ($P = 0.0027$) for 10% of comparisons; 2) cattle and deer were separate ($P < 0.0001$) for 94% of comparisons and overlapped ($P = 0.0656$) for 6% of comparisons; and 3) deer and nilgai were separate ($P < 0.0001$) for 10% of comparisons, individuals of deer and nilgai had similar diets ($P \leq 0.0105$) for 60% of comparisons, and overlapped ($P \geq 0.0903$) for 30% of comparisons (Table 4.1; Fig. 4.4).

Dietary niche space placement along the dietary niche continuum

Across seasons, years, and the South Texas landscape: 1) cattle consumed an average of 80–88% C_4 forages in their diet (e.g., classified as grazers along the continuum); 2) nilgai consumed an average range of 19–38% C_4 forages in their diet (e.g., classified as browser-intermediate feeder along the continuum); and 3) deer consumed an average of 3–11% C_4 forages in their diet (e.g., classified as browsers along the continuum; Fig. 4.5).

Table 4.1. Seasonal dietary niche comparisons between cattle, deer, and nilgai on 4 East Foundation ranches in South Texas, autumn 2012 – spring 2015. The dietary niche was analyzed for each species as the linear combination of the fecal carbon and nitrogen stable isotope signatures in a multivariate analysis of variance (MANOVA). The MANOVA analyzed variation within and between species, which is the definition of dietary niche width. Because I had a significant species*site*season*year interaction ($P < 0.0001$), every site was analyzed separately for each season, each year (No. of Comparisons). Unless the *P*-value was less than 0.0001, the stable isotope dietary niche was not completely separate between species. Therefore, under Overlap: 1) no indicates the dietary niche was completely separate between species compared; 2) similar indicates individuals of both species compared had similar diets (although not statistically significant dietary niche overlap at $\alpha = 0.05$); and 3) yes indicates dietary niches overlapped.

Species Comparison	No. of Comparisons	Overlap	*P*
Autumn 2012–2014			
Cattle versus Nilgai	7	No	< 0.0001
	0	Similar	—
	0	Yes	—
Cattle versus Deer	16	No	< 0.0001
	1	Similar	= 0.0006
	1	Yes	= 0.0525
Deer versus Nilgai	0	No	—
	3	Similar	$0.0012 < P < 0.0231$
	4	Yes	$0.2845 < P < 0.9141$
Spring 2013–2015			
Cattle versus Nilgai	6	No	< 0.0001
	1	Similar	= 0.0007
	0	Yes	—
Cattle versus Deer	18	No	< 0.0001
	0	Similar	—
	0	Yes	—
Deer versus Nilgai	3	No	< 0.0001
	3	Similar	$0.0010 < P < 0.0436$
	1	Yes	= 0.5655

Table 4.1. Continued.

Species Comparison	No. of Comparisons	Overlap	*P*
Winter 2013–2015			
Cattle versus Nilgai	9	No	< 0.0001
	1	Similar	= 0.0027
	0	Yes	—
Cattle versus Deer	17	No	< 0.0001
	0	Similar	—
	1	Yes	= 0.0656
Deer versus Nilgai	1	No	< 0.0001
	6	Similar	0.0002 < *P* < 0.0105
	3	Yes	0.0903 < *P* < 0.9203

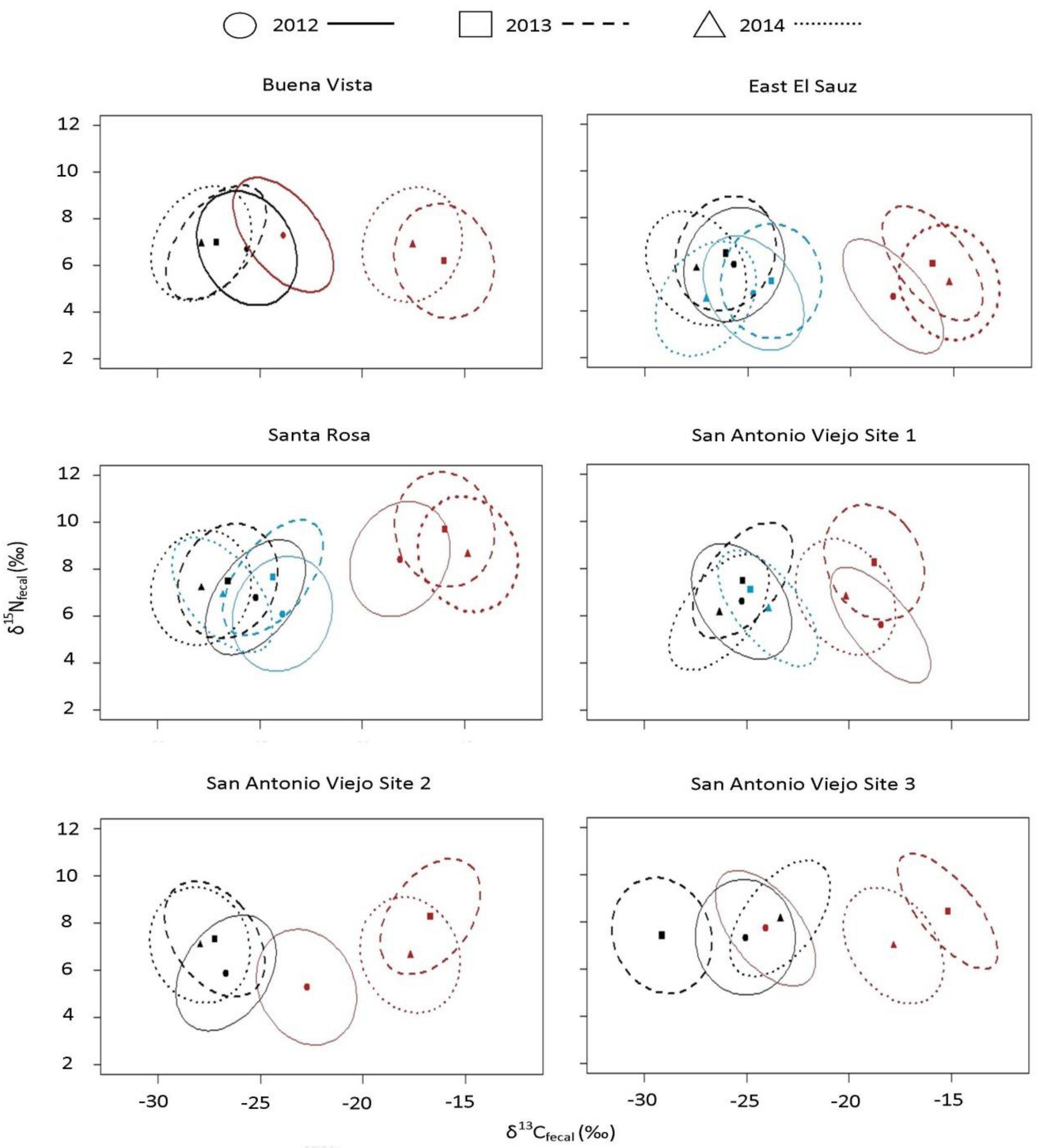

Figure 4.2. Mean fecal carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope signature (circle, square, or triangle) and 95% fecal stable isotope confidence ellipses for cattle (red), deer (black), and nilgai (blue) on 4 East Foundation ranches in South Texas, autumn 2012–2014. At San Antonio Viejo Site 1 during 2012–2013, only three nilgai samples were collected (blue square), thus no confidence ellipse was drawn for these time periods. The further the ruminants ellipse is to the right (-15 ‰), the higher percentage of grasses, the further to the left (-30 ‰), the higher percentage of browse/forbs in the ruminants diet.

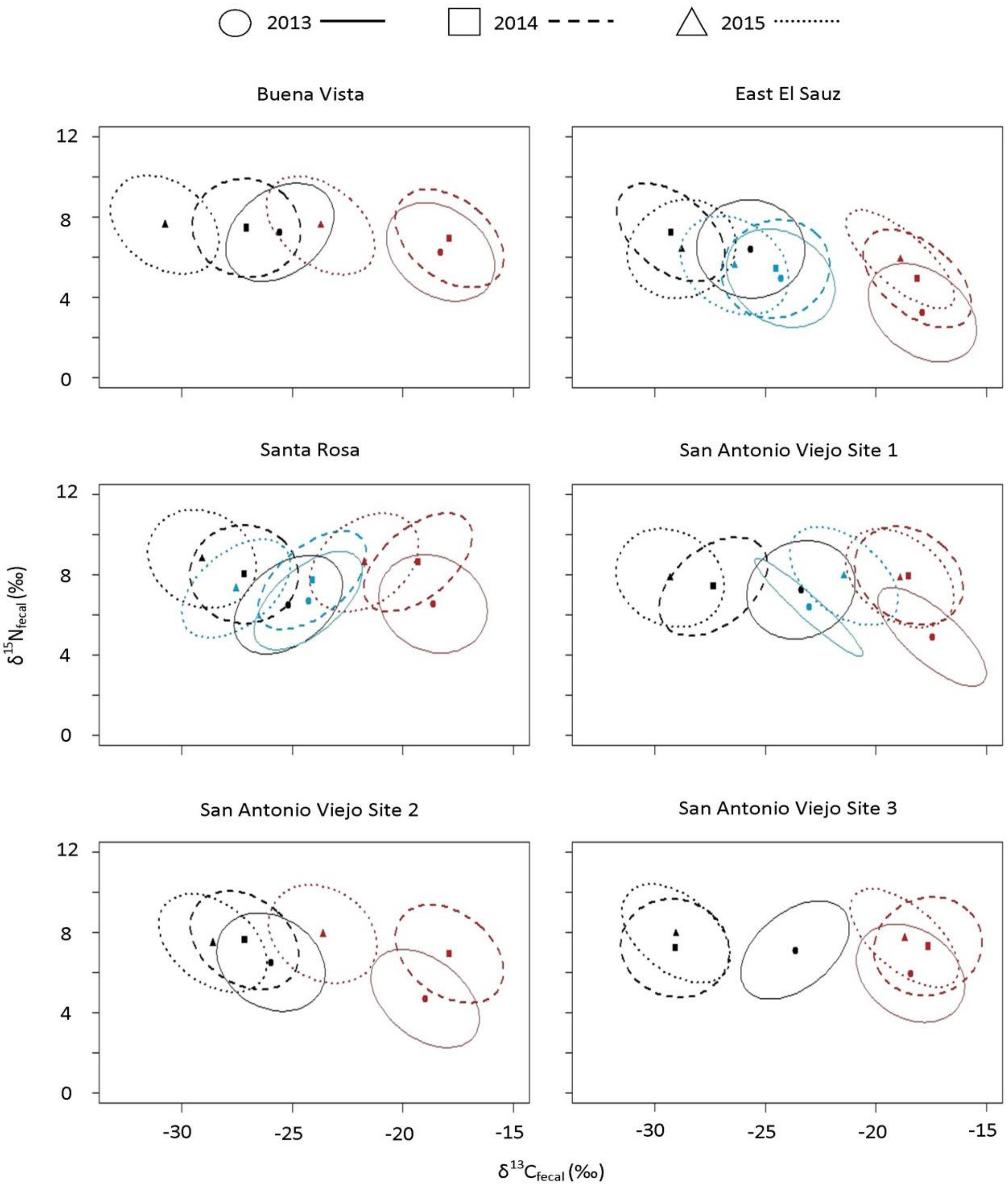

Figure 4.3. Mean fecal carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope signature (circle, square, or triangle) and 95% fecal stable isotope confidence ellipse for cattle (red), deer (black), and nilgai (blue) on 4 East Foundation ranches in South Texas, spring 2013–2015. At San Antonio Viejo Site 1 during 2014, no nilgai samples were collected. The further the ruminants ellipse is to the right (-15 ‰), the higher percentage of grasses, the further to the left (-30 ‰), the higher percentage of browse/forbs in the ruminants diet.

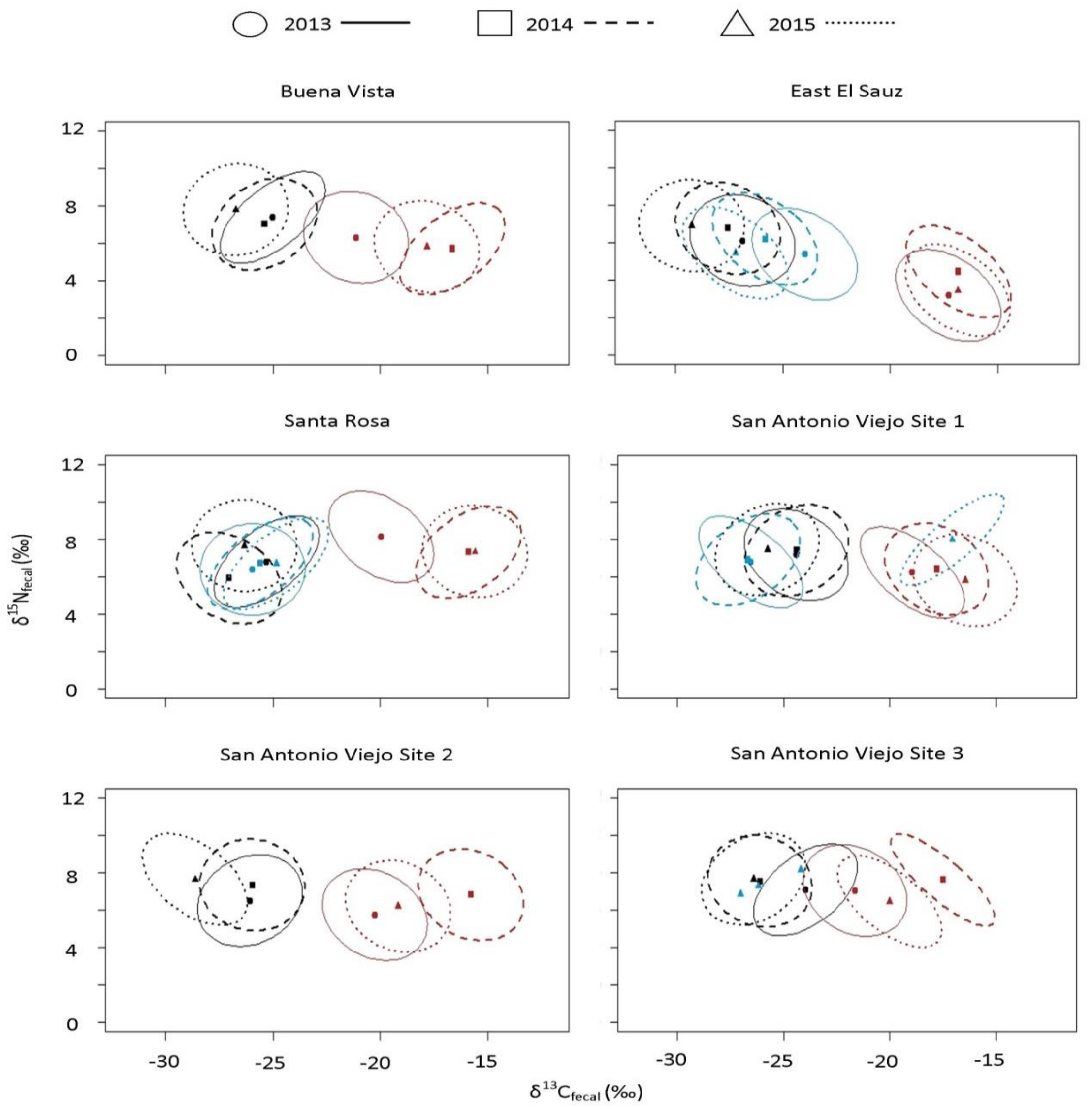

Figure 4.4. Mean fecal carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope signature (circle, square, or triangle) and 95% fecal stable isotope confidence ellipse for cattle (red), deer (black), and nilgai (blue) on 4 East Foundation ranches in South Texas, winter 2013–2015. At San Antonio Viejo Site 3 during winter 2015, three nilgai samples were collected (blue triangles), thus no confidence ellipse was drawn for this time period (this was the first occurrence of collecting nilgai samples at this site). The further the ruminants ellipse is to the right (-15 ‰), the higher percentage of grasses, the further to the left (-30 ‰), the higher percentage of browse/forbs in the ruminants diet.

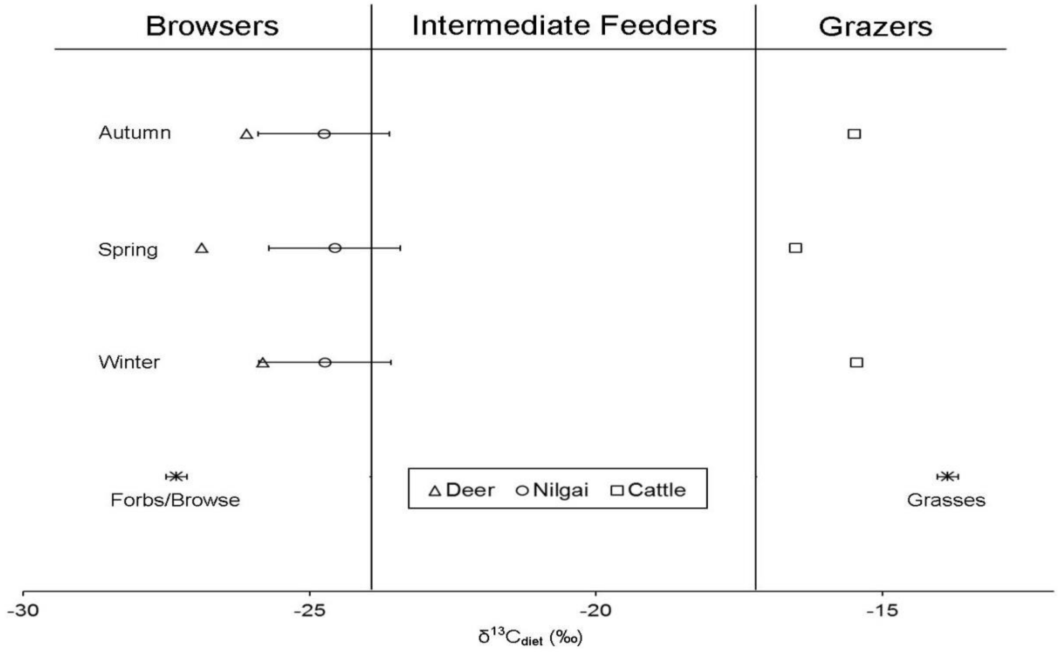

Figure 4.5. Seasonal mean carbon stable isotope ($\delta^{13}C$) signature for cattle, deer, and nilgai on 4 East Foundation ranches in South Texas, autumn 2012 – spring 2015; each row corresponds to listed season. Carbon stable isotope was analyzed for fresh fecal samples collected during each season, and corrected (adding diet-feces fractionation rate) to reflect diet consumed. The fractionation rate was known for deer and cattle, but not nilgai. Thus the lines associated with the symbol for nilgai, represent the possible range of carbon stable isotope diet values for nilgai based on fractionation rates of deer and cattle (e.g., nilgai are intermediate feeders, therefore I assumed nilgai fractionation rate should be between deer and cattle). The asterisks at the bottom are the average stable isotope signature of forages in South Texas (averaged across autumn and spring seasons, and years, 2012–2014). Proximity of vertical alignment of the ruminant $\delta^{13}C_{diet}$ signature to $\delta^{13}C$ of forage class (e.g., forbs/browse or grasses), indicates a higher percentage in the ruminant diet. The carbon isotope signature in a landscape dominated by C_4 grasses allows determination of ruminant dietary niche space along the dietary niche continuum.

Discussion

My results largely agreed with classification of deer as browsers and cattle as grazers. However my results did not agree with previous classification of nilgai as intermediate feeders more similar to cattle than deer along the dietary niche continuum. Previous research in South Texas indicated nilgai selected mostly for grasses (diets were 60–70% grasses; Sheffield, 1983; Stuth and Sheffield, 1981), thus nilgai dietary niche space should have been more similar to grazers (Fulbright and Ortega-S., 2013). Yet my research determined the opposite – nilgai dietary niche space is actually more similar to browsers. While cattle selected for grasses, nilgai may not select for grasses when standing crop of herbaceous forage is below potential production.

During this study, drought conditions were predominant (Fig. 2.4, pg. 28) and standing crop of herbaceous vegetation across study sites was below potential range production (Table 2.2, pg. 36; USDA-NRCS, 2011a, b). Nilgai are intermediate feeders, therefore are highly adaptable to shifting vegetation communities because reversible modifications within digestive anatomy allows intermediate feeders to switch between highly digestible forages (e.g., forbs) and less digestible forages (e.g., grasses) based on availability within the vegetation community (Hofmann, 1973). These adaptive capabilities do not extend to species which have evolved to occupy the extreme ends (e.g., deer and cattle) of the dietary niche continuum.

Unless bare ground was prevailing at study sites (e.g., Buena Vista and San Antonio Viejo site 3 during 2012–2013), cattle and deer occupied the extreme ends of the dietary niche continuum. Nilgai were mostly closer to browsers; however during non-drought conditions, nilgai stable isotope dietary niche space shifted closer to cattle (e.g., consumed higher percentage of grasses) at San Antonio Viejo site 1. These results exemplify the adaptive potential of intermediate feeders to switch between forage classes (e.g., diet high in browse/forbs to diet high in grasses) with fluctuating availability of forages during this study.

In stochastic environments, such as the semiarid landscape of South Texas, intermediate feeders do not occupy a static space along the dietary niche continuum; their dietary niche space fluctuates with forage availability in the perpetually shifting vegetation community (Fig. 4.6). In contrast, species at extreme ends of the browsing-grazing niche continuum have evolved morphological characteristics which constrain them to an invariable space along the continuum, regardless of fluctuating conditions (with exception of extreme forage limitations). Hence, intermediate feeders have a higher potential of out-competing sympatric species restricted to extreme ends of the dietary niche continuum. Furthermore, especially in stochastic regions, but also applies to introduction of intermediate feeders into new environments, morphological characteristics of intermediate feeders may not be a reliable resource to determine if diets of intermediate feeders will be similar to diets of other sympatric species, whether they are grazers or browsers.

While I agree, based on my results, that morphological characteristics may be valid to classify species at extreme ends of the browsing-grazing niche continuum; my results provide evidence based on diet composition under field conditions that classifying intermediate feeders based on morphological characteristics may not always be accurate (e.g., because of reversible modifications within digestive anatomy). My findings highlight the need to conduct long term research, under a variety of environmental and vegetation community conditions, to determine patterns and trends of intermediate feeders' diets before determining their niche space along the dietary niche continuum.

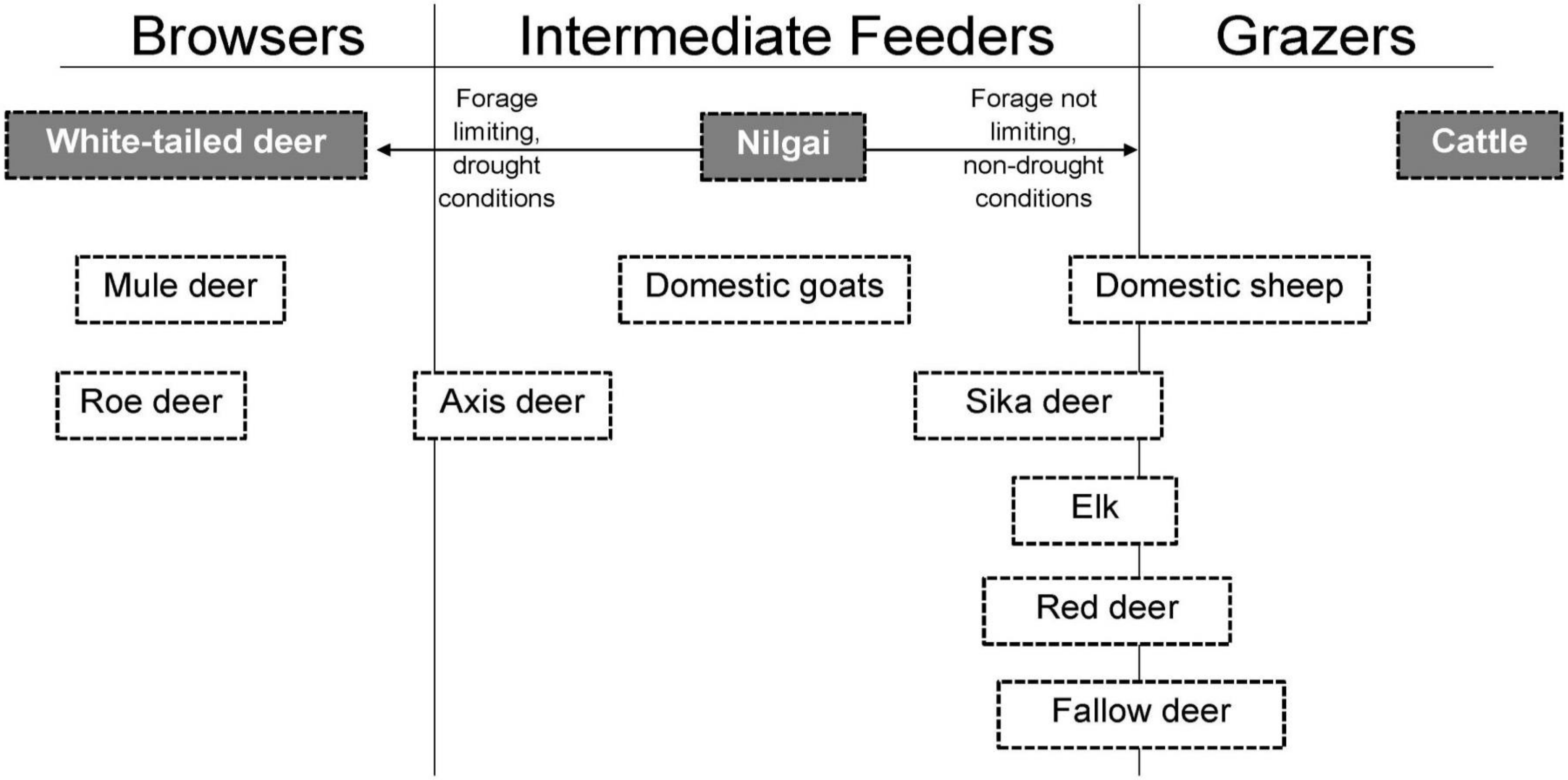

Figure 4.6. Revised relationship of dietary niche space of cattle, deer, and nilgai across the South Texas landscape based on results of this study. Intermediate feeders, nilgai, have the adaptive ability to switch among forages classes (e.g., browse/forbs or grasses) based on forage availability. These adaptive capabilities do not extend to species which have evolved to occupy the extreme ends (e.g., deer and cattle) of the dietary niche continuum. Along the continuum, progressing from browsers (far left) to grazers (far right), the percentage of grasses in the diet increases. Figure adapted, with permission, from Fulbright and Ortega-S. (2013).

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Appendix A. Publications included in quantitative literature review. Citation and source of publication from which data were extracted. Data were quantitatively analyzed in the marked data set(s).

Citation, Source	Data Set			
	Forbs	Woody Plants	Space Use	Diet Overlap
Anderson and Scherzinger 1975, J Range Manage 28, 120–125.			X	
Austin and Urness 1986, J Range Manage 39, 18–21.	X	X		
Austin et al. 1983, J Range Manage 36, 589–593.			X	
Barrett 1982, J Range Manage 35, 342–346.			X	
Bates et al. 2009, Rangeland Ecol Manag 62, 98–110.	X	X		
Beck and Peek 2005, Rangeland Ecol Manag 58, 135–147.				X
Bélanger and Picard 1999, J Range Manage 52, 332–338.		X		
Berentsen et al. 2014, Eur J Wildl Res 60, 161–170.			X	
Borchert *et al.* 1989, Ecology 70, 389–404.		X		
Bratton 1979, Proceeding of the Annual Conference of Southeastern Fish and Wildlife Agencies 33, 305–312.	X	X		
Bratton et al. 1980, Environ Manage 4, 433–448.	X	X	X	
Brown 1984, MS Thesis University of Arizona.		X	X	
Campbell and Johnson 1983, J Range Manage 36, 488–491.				X
Clary 1999, J Range Manage 52, 218–227.	X	X		
Coe et al. 2001, J Range Manage 54, A51–A76.			X	
Compton et al. 1988, J Wildl Manag52, 544–548.			X	
Cooper et al. 2008, Agr Ecosyst Environ 127, 85–92.			X	
Currie et al. 1977, J Range Manage 30, 352–356.				X
Dasmann 1949, J Range Manage 2, 206–212.				X
Dusek 1975, J Wildl Manag39, 605–616.			X	X
Dusek et al. 1989, Wildlife Monogr 104, 3–68.			X	
Elliott and Barrett 1985, J Range Manage 38, 546–550.				X
Evans et al. 2004, J Range Manage 57, 539–545.	X			

Appendix A. Continued.

Citation, Source	Data Set			
	Forbs	Woody Plants	Space Use	Diet Overlap
Findholt *et al.* 2004, Transactions of the 69th North American Wildlife and Natural Resources Conference				X
Fullmer 1994, Proceedings of the 15th Annual Forest Vegetation Management Conference.	X	X		
Galindo–Leal et al. 1993, Southwest Nat 38, 127–135.			X	
Gallina 1993, J Range Manage 46, 487–492.				X
Ganskopp et al. 2004, J Range Manage 57, 161–168.		X		
Hall et al. 1992, J Range Manage 45, 503–506.		X		
Hanley and Hanley 1982, J Range Manage 35, 152–158.				X
Hansen and Clark 1977, J Wildl Manag41, 76–80.				X
Hansen and Reid 1975, J Range Manage 28, 43–47.				X
Hansen et al. 1977, J Range Manage 30, 116–118.				X
[*]Hines *et al. unpublished data*	X			
Hoffmann and Stanley 1978, J Range Manage 31, 412–416.	X			
Hood and Inglis 1974, J Wildl Manag38, 488–498.			X	
Hubbard and Hansen 1976, J Range Manage 29, 389–392.				X
Jenks et al. 1996, Acta Theriol 41, 287–306.				X
Karl and Doescher 1998, J Range Manage 51, 147–151.		X		
Kay and Bartos 2000, J Range Manage 53, 145–153.	X	X		
Kie et al. 1991, J Wildl Manag55, 665–674.			X	
Kingery et al. 1996, J Range Manage 49, 8–15.				X
Koerth et al. 1985, Southwest Nat 30, 579–587.			X	
Kohl *et al.* 1987, Proceeding of the Annual Conference of Southeastern Fish and Wildlife Agencies 41, 299–302.			X	
Krämer 1973, J Wildl Manag37, 288–300.			X	
Kranz and Linder 1973, J Range Manage 26, 263–265.			X	

Appendix A. Continued.

Citation, Source	Data Set			
	Forbs	Woody Plants	Space Use	Diet Overlap
Krueger and Windward 1974, J Range Manage 27, 450–453.	X	X		
LeCain et al. 2002, Agr Ecosyst Environ 93, 421–435.	X	X		
Loeser et al. 2007, Rangeland Ecol Manag 58, 234–238.	X			
Loft et al. 1991, Conserv Biol 21, 87–97.			X	
Lucich and Hansen 1981, J Range Manage 34, 72–73.				X
Lutz 1930, J Agric Res 41, 561–570.	X	X		
MacCracken and Hansen 1981, J Range Manage 34, 242–243.				X
Mackie 1970, Wildlife Monogr 20, 3–79.			X	
Martinez M. et al. 1997, J Range Manage 50, 253–257.				X
McDonald and Fiddler 1999, US Department of Agriculture. PSW-RP-242.	X	X		
McMahan 1966, J Wildl Manag30, 151–162.			X	
Moore and Terry 1979, Proceeding of the Annual Conference of Southeastern Fish and Wildlife Agencies 33, 279–287.		X		
Ngugi et al. 1992, J Range Manage 45, 542–545.				X
Ortega et al. 1997a, J Range Manage 50, 615–621.		X		
Ortega et al. 1997b, J Range Manage 50, 622–630.				X
Peterson et al. 2014, Rangeland Ecol Manag 67, 78–87.	X	X		
Ragotzkie and Bailey 1991, J Range Manage 44, 487–490.			X	
Reardon et al. 1978, J Range Manage 31, 40–42.			X	
Roberts and Tiller 1985, Wildlife Soc B 13, 248–252.		X	X	
Short and Knight 2003, J Range Manage 56, 213–217.	X			
Smith and Coblentz 2010, Northwest Sci 84, 315–326.			X	
Stewart et al. 2002, J Mammal 83, 229–244.			X	
Suring and Vohs 1979, J Wildl Manag43, 610–619.			X	
Teer et al. 1965, Wildlife Monogr 15, 3–62.			X	

Appendix A. Continued.

Citation, Source	Data Set			
	Forbs	Woody Plants	Space Use	Diet Overlap
Thilenius and Hungerford 1967, J Wildl Manag31, 141–145.	X	X		
Thill 1984, J Wildl Manag48, 788–798.				X
Thill and Martin 1986, J Wildl Manag50, 707–713.				X
Thill and Martin 1989, J Wildl Manag53, 540–548.				X
Torstenson et al. 2006, Rangeland Ecol Manag 59, 80–87.				X
Towne et al. 2005, Ecol Appl 15, 1550–1559.	X	X		
Wagoner et al. 2013, J Wildl Manag77, 897–907.	X			
Wallace and Krausmann 1987, J Range Manage 40, 80–83.			X	
Wilcox et al. 2010, Rangeland Ecol Manag 63, 203–222.	X			
Willms et al. 1979, J Range Manage 32, 299–304.		X	X	X
Willms et al. 1980, J Range Manage 33, 55–59.	X	X		X
Wood and Blackburn 1984, J Range Manage 37, 303–308.	X			
Yeo et al. 1993, J Range Manage 46, 245–250.			X	
Zimmerman and Neuenschwander 1984, J Range Manage 37, 104–110.	X	X		
zu Dohna *et al.* 2014, Prev Vet Med 113, 447–456.			X	

[*] I included unpublished data from the study described in Chapter II of this dissertation.

Appendix B. List of non-preferred deer forbs, determined from previous research regarding forb palatability to deer in South Texas, identified on 4 East Foundation ranches, autumn 2012 – spring 2015.

Scientific name	Common name
Asteraceae	
Ambrosia confertiflora	False ragweed
Cirsium texanum	Texas thistle
Florestina tripteris	Three-lobed florestina
Grindelia microcephala	Small flowered gumweed
Heterotheca subaxillaris	Camphor weed
Palafoxia hookeriana	Showy palafoxia
Palafoxia rosea	Rose palafoxia
Palafoxia texana	Texas palafoxia
Thymophylla tenuiloba	Bristleleaf dogweed
Thymophylla tephroleuca	Ashy dogweed
Verbesina encelioides	Cowpen daisy
Viguiera stenoloba	Skeleton-leaf goldeneye
Boraginaceae	
Tiquilia canescens	Oreja de perro
Chenopodiaceae	
Salsola tragus	Prickly russian thistle (tumbleweed)
Euphorbiaceae	
Croton capitatus	Wooly croton
Croton coryi	Cory's croton
Croton glanulosis	Tropic croton
Croton glanulosis var. septentrionalis	Northern croton
Croton leucophyllus	White-leaf croton
Croton texensis	Texas croton
Hydrophyllaceae	
Nama hispidum	Sandbell
Lamiaceae	
Monarda fruticulosa	Shrubby beebalm
Monarda punctata	Spotted beebalm
Malvaceae	
Abutilon theophrasti	Velvet leaf
Papaveraceae	
Argemone albiflora	White prickly poppy
Nyctaginaceae	
Acleisanthes obtusa	Berlander's trumpet
Allionia incarnata	Trailing four o'clock
Nyctaginea capitata	Scarlet musk flower

Appendix B. Continued.

Scientific name	Common name
Solanaceae	
Solanum eleagnifolium	Silverleaf nightshade
Verbenaceae	
Phyla incisa	Sawtooth Frog-Fruit
Phyla strigulosa	Common frog fruit

Appendix C. List of most common forbs preferred by white-tailed deer, determined from previous research regarding forb palatability to deer in South Texas, identified on 4 East Foundation ranches, autumn 2012 – spring 2015.

Scientific name	Common name
Native annual	
Amaranthus polygonoides	Low amaranth
Aphanostephus ramosissimus var. ramosissimus	Lazy daisy
Aster subulatus var. ligulatus	Prairie aster
Chamaecrista fasciculata	Partridge pea
Chenopodium pratericola	Desert goosefoot
Croptilon rigidifolium	Scratch daisy
Diaperia candida	Rabbit tobacco
Diodia teres	Rough buttonweed
Eriogonum multiflorum	Common buckwheat
Euphorbia glyptosperma	Ridgeseed euphorbia
Froelichia drummondii	Snake cotton
Helianthus argophyllus	Silverleaf sunflower
Helianthus praecox ssp. runyonii	Sand sunflower
Mollugo verticillata	Indian chickweed
Rayjacksonia phyllocephala	Camphor daisy
Salicornia bigelovii	Glasswort
Suaeda linearis	Annual seepweed
Tidestromia lanuginosa	Woolly tidestromia
Xanthisma texanum	Texas sleepy daisy
Native perennial	
Abutilon abutiloides	Shruby indian mallow
Abutilon sp.	White flower indian mallow sp.
Acalypha radians	Cardinal feather
Allium canadense	Wild onion
Ambrosia psilostachya	Western ragweed
Batis maritima	Saltwort
Boerhavia coccinea	Scarlet spiderling
Borrichia frutescens	Sea ox eye
Callirhoe involucrata var. lineariloba	Winecup
Chamaecrista calycioides	Woodland sensitive pea
Chamaecrista flexuosa var. texana	Texas senna
Commelina erecta var. angustifolia	Widow's tear
Conoclinium coelestinum	Blue mistflower
Cooperia drummondii	Rainlily
Dalea aurea	Golden dalea
Dalea pogonathera	Bearded dalea

Appendix C. Continued.

Scientific name	Common name
Desmanthus virgatus var. depressus	Creeping bundle flower
Ditaxis humilis	Wild mercury
Engelmannia peristenia	Engelmann's daisy
Erigeron procumbens	Prostrate fleabane
Evolvulus alsinoides var. angustifolius	Slender evolvulus
Evolvulus nuttallianus	Hairy evolvulus
Evolvulus sericeus	Silky evolvulus
Galactia canescens	Hoary milkpea
Heliotropium confertifolium	Crowded heliotrope
Hymenopappus scabiosaeus	Old plainsman
Indigofera miniata	Scarlet indigo
Isocoma drummondii	Goldenweed
Justicia pilosella	Tube tounge
Mimosa microphylla	Catclaw sensitive briar
Oxalis dellenii	Yellow wood sorrel
Oxalis frutescens subsp. angustifolia	Narrow leaf shrubby wood sorrel
Phyllanthus polygonoides	Knotweed leaf flower
Physalis cinerascens	Yellow ground cherry
Physaria argyraea	Silver bladderpod
Pomaria austrotexana	South Texas rushpea
Ratibida columnifera	Mexican hat
Rhynchosia americana	American snoutbean
Richardia brasiliensis	Tropical mexican clover
Richardia tricocca	Prairie mexican clover
Schrankia latidens	Karnes sensitive briar
Sida Ciliaris var. mexicana	Bracted sida
Sida cordata	Heartleaf fanpetals
Sida lindheimeri	Showy sida
Sida physocalyx	Spade leaf sida
Solanum americanum	American nightshade
Sphaeralcea lindheimeri	Woolly globe mallow
Sphaeralcea pedatifida	Palm leaf globe mallow
Stemodia lanata	Woolly stemodia
Suaeda tampicensis	Tampico seepweed
Tephrosia lindheimeri	Lindheimer tephrosia
Viguiera stenoloba	Skeleton leaf golden eye
Waltheria indica	Hibera del soldado
Zornia bracteata	Bracted zornia

Appendix C. Continued.

Scientific name	Common name
Native annual or perennial	
Gaillardia pulchella	Indian blanket
Lepidium virginicum var. medium	Virginia pepperweed
Portulaca pilosa	Shaggy portulaca
Zornia reticulata	Net leaf rabbit's ears
Non-native annual	
Cyclospermum leptophyllum	Slim lobe celery
Phyllanthus tenellus	Tender leaf flower
Portulaca oleracea	Common purslane
Non-native perennial	
Calyptocarpus vialis	Straggler daisy
Sida abutifolia	Spreading sida

Appendix D. List of grasses identified on 4 East Foundation ranches, autumn 2012 – spring 2015.

Scientific name	Common name
Native annual	
Aristida oligantha	Oldfield threeawn
Cenchrus echinatus	Southern sandbur
Panicum capillare	Fall witchgrass
Native Perennial	
Andropogon virginicus	Broomsedge bluestem
Bouteloua hirsuta	Hairy grama
Chloris cucullata	Hooded windmillgrass
Dichanthelium oligosanthes	Scribner's panicgrass
Digitaria arenicola	Sand witchgrass
Digitaria texana	Texas crabgrass
Distichlis spicata	Inland saltgrass
Eragrostis curtipedicellata	Gummy lovegrass
Eragrostis secundiflora	Red lovegrass
Eragrostis trichodes	Sand lovegrass
Heteropogon contortus	Tanglehead
Monanthochloë littoralis	Shoregrass
Nassella leucotricha	Texas wintergrass
Panicum capillarioides	Southern witchgrass
Panicum obtusum	Vine mesquite
Panicum virgatum	Switchgrass
Paspalum monostachyum	Gulfdune paspalum
Paspalum plicatulum	Brownseed paspalum
Paspalum setaceum	Thin paspalum
Schedonnardus paniculatus	Tumblegrass
Schizachyrium littorale	Seacoast bluestem
Schizachyrium scoparium	Little bluestem
Setaria leucopila	Plains bristlegrass
Setaria parviflora	Knotroot bristlegrass
Setaria reverchonii subsp. firmula	Knotgrass
Spartina patens	Marshhay cordgrass
Spartina spartinae	Gulf cordgrass
Sporobolus cryptandrus	Sand dropseed
Sporobolus purpurascens	Purple dropseed
Urochloa ciliatissima	Fringed signalgrass
Native annual or perennial	
Aristida purpurea	Purple threeawn
Cenchrus spinifex	Coastal sandbur
Sporobolus pyramidatus	Whorled dropseed
Sporobolus sp.	Dropseed species

Appendix D. Continued.

Scientific name	Common name
Non-native annual	
Dactyloctenium aegyptium	Durban crowfoot
Digitaria sanguinalis	Hairy crabgrass
Tragus berteronianus	Spike burgrass
Non-native perennial	
Cynodon dactylon	Bermudagrass
Dichanthium annulatum	Kleberg bluestem
Eragrostis lehmanniana	Lehmann's lovegrass
Paspalum dilatatum	Dallisgrass
Pennisetum ciliare	Buffelgrass

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PUBLICATIONS

Hines, S.L. 2016. Development of a biologically centered habitat monitoring technique: SPIDER transect method. Southeastern Naturalist *Accepted May 2016.*

Hines, S.L., T.E. Fulbright, J.A. Ortega-S., D.G. Hewitt, T.W. Boutton, and A. Ortega-S. Jr. 2015. Dietary competition among nilgai, cattle, and deer: what we can learn from atoms. Texas Landowner Magazine Winter 2015:70-71.
Nominated November 2015: Popular Article Publication Award with Texas Chapter of the Wildlife Society

Hines, S.L. and A.E. Hershey. 2011. Do channel restoration structures promote ammonium uptake and improve macroinvertebrate-based water quality classification in urban streams? Inland Waters 1:133-145.

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