

**DISENTANGLING MECHANISMS AND DRIVERS OF COMPETITION BETWEEN
WHITE-TAILED DEER AND CATTLE**

A Thesis

by

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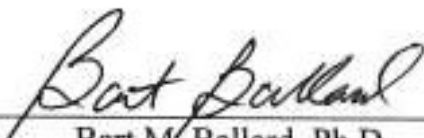
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ABSTRACT

Disentangling Mechanisms and Drivers of Competition between

White-Tailed Deer and Cattle

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Competition is a complex ecological process that can impact interspecific and intraspecific interactions, having trophic and evolutionary effects. Competition is commonly expressed through two recognized mechanisms: exploitative and interference competition. These mechanisms are often co-occurring within systems, making it difficult to develop a mechanistic understanding of competition and complicating predictions of population level impacts as a result. Therefore, in effort illuminate this complex process, we investigated the influences of competition with cattle (*Bos taurus*) on white-tailed deer (*Odocoileus virginianus*) population nutritional performance and the mechanistic processes through which these effects occur. During November and December, we conducted annual deer captures between 2017–2021 on four cattle ranches across South Texas, where we recorded nutritional metrics such as antler scores, lactation status, body mass, and subcutaneous rump fat depth. We linked these nutritional metrics to cattle stocking rates and environmental conditions, and determined that male nutritional metrics were more sensitive cattle competition while female nutritional metrics were primarily driven by age and reproductive status. Furthermore, our results suggest the nutritional metrics of antler scores and rump fat depth were more driven by external factors while body mass was

primarily influenced by age. To evaluate the mechanisms driving these nutritional effects, we deployed 19 global positioning system collars in March 2020 on mature female white-tailed deer captured in northern most portion of the largest ranch. This study site was vacant of cattle for two years before cattle were experimentally restocked in November 2020. This allowed us to monitor development of exploitative and interference competition through changes in white-tailed deer behavior and space-use. Our results suggest interference competition occurred rapidly independent of exploitative competition, resulting in deer utilizing poor quality habitat and brushier sites to avoid interacting with cattle.

PREVIEW

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Contributors

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The white-tailed deer data analyzed for Chapter 1 was collected, in part, by Seth Rankins, Miranda Hopper, Drs. Jacob L. Dykes, Randall W. DeYoung, J. Alfonso Ortega-S, David G. Hewitt. Cattle stocking data from East Foundation properties that was analyzed in both chapters was provided by Molli Foxley, Zane Herrin, Garrett Stribling, Eddie Reyna.

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CHAPTER 1

NUTRITIONAL CONSEQUENCES OF COMPETITION BETWEEN CATTLE AND WHITE-TAILED DEER¹

Abstract

Understanding the interactive effects of competition and environmental conditions on animal nutrition is important for monitoring population performance. It is suspected the competition between livestock and wildlife can reduce nutritional condition in wildlife, however environmental conditions may mediate this effect. We examined this interaction by linking metrics of nutritional condition (body mass, rump fat, antler scores) and reproduction (lactation status) of 533 male and 629 female white-tailed deer (*Odocoileus virginianus*) captured during October–November from 2017–2021 with cattle (*Bos taurus*) stocking rates and environmental conditions (such as percentage of sand in the soil, rainfall, herbaceous biomass, and brush cover) georeferenced to the capture locations across four South Texas ranches. We fitted generalized linear mixed models to estimate the interactive effects of stocking rates and environmental conditions on white-tailed deer nutritional and reproductive metrics. Cattle stocking rates during this five-year period ranged between 0–23.52 AU/ km²/year and did not influence lactation status or male and female body mass. However, antler size decreased 1.67 cm for every AU/ km²/year increase in cattle stocking rates ($\beta = -0.057$; 85% CI: -0.111 to -0.001). Male rump fat also decreased with stocking rates but the effect was strongly influenced by environmental conditions; during dry years and sandier soils male deer had little rump fat regardless of stocking rates. These results indicate a sex-specific response in the nutritional consequence of

¹This Chapter is written in the style of *Oecologia*

white-tailed deer–cattle competition, as only male white-tailed deer nutritional metrics were negatively affected by cattle stocking rates, while female condition was largely driven by reproductive activity.

Introduction

Ecological niche overlap and resource scarcity drive competition within and among species, and can have broad impacts on population dynamics and physiological characteristics of individuals (Abrams 1987; Sebens 1987; Dutta et al. 2014; Costa-Pereira et al. 2018). Many species life history traits, such as reproduction, survival, and growth, are tied to an organism's nutrition (Sebens 1987; Parker et al. 2009; DeGabriel et al. 2014; Oates et al. 2021), and therefore can be influenced by competition through its ability to manipulate resource acquisition (Mitchell et al. 1990; De Roos et al. 2009; Lane et al. 2010). For example, competitors can increase the energetic demands to acquire resources by limiting access to and abundance of resources within their system (Belant et al. 2006; Chase et al. 2016; Oates et al. 2021). Furthermore, subordinate competitors may employ energetically costly avoidance behaviors to limit contact with the dominant competitors (Loft et al. 1991; Durant 2000; Cooper et al. 2008). The intensity of these competitive processes and the resulting nutritional consequences are often density-dependent, as more individuals within the competitive interaction can increase the frequency of encounters and use of limited resources (Stewart et al. 2005; Denac 2006; Reiskind and Lounibos 2009). Frequently, these density-dependent effects are observed within intraspecific competitive interactions due to individuals of a species sharing a fundamental niche (Stewart et al. 2005; Denac 2006; Reiskind and Lounibos 2009). However, niche partitioning and character

displacement reduce interspecific competition, making these effects less common (Abrams 1987; Finke and Snyder 2008).

Resource limitation may abate tactics of competition avoidance, increasing niche overlap between species and intensifying competition of shared resources (Krämer 1973; Belant et al. 2006; Chase et al. 2016). As a result, there may be direct nutritional consequences for the subordinate species. For example, in Alaska, USA, competition between brown bears (*Ursus arctos*) and black bears (*Ursus americanus*) increased during low salmon abundance and resulted in reduced body condition and reproduction of black bears (Belant et al. 2006). Resource scarcity can be triggered by seasonal and extreme climatic events (Haddad et al. 2002; Wang et al. 2003; Prugh et al. 2018), overabundance of consumers (Allombert et al. 2005; Mysterud 2006), and other disturbance events such as disease and anthropogenic development (Leu et al. 2008; Creissen et al. 2016).

Droughts are a common driver of resource scarcity in arid and semi-arid ecosystems and are increasing in frequency and intensity with climate change (Schwinning and Sala 2004; Chiang et al. 2021). The semi-arid landscape of South Texas experienced five droughts between 2011-2021, with four of those years recording average annual rainfall 100 mm below the 30-year normal for the region (PRISM Climate Group 2021). The extreme variability in precipitation in this landscape drives vegetation productivity (Fulbright et al. 2021), population dynamics in wildlife (Kie and White 1985; Cooper et al. 2009; Foley et al. 2012), and alterations of land use practices (Montalvo et al. 2020). Research suggests cattle (*Bos taurus*) grazing may have direct nutritional consequence for white-tailed deer (*Odocoileus virginianus*) if resources become limited (Thill and Martin 1986; Chaikina and Ruckstuhl 2006; Hines et al. 2021; Fulbright et al. 2021). These species operate on opposing ends of the browser-grazer dietary strategy continuum

(Fulbright and Ortega-S. 2013; Esmaeili et al. 2021). However, dietary overlap increases when forage becomes limited due to overgrazing or environmental stochasticity (Ortega et al. 1997; Chaikina and Ruckstuhl 2006; Hines et al. 2021). Furthermore, *Odocoileus sp.* avoid contact with cattle and when encountered often move away, utilize rugged habitat, and, in extreme instances, abandon their home ranges (Hood and Inglis 1974; Loft et al. 1991, 1993; Cooper et al. 2008). Therefore, it is possible that competition with cattle coupled with resource limitations may have direct nutritional consequences for white-tailed deer.

Assessing these nutritional effects in white-tailed deer requires identifying biological and physiological traits that advertise individual nutritional condition. As nutrition can often influence life history traits of organisms (Sebens 1987; Parker et al. 2009; Ayotte et al. 2020; Oates et al. 2021), individual condition can be measured through characteristics of growth, development, and reproductive status such as antler sizes, lactation rates, fat deposition, and body mass. Male white-tailed deer antlers are a secondary sexually selected trait that are disposed and regrown yearly and are nutritionally costly to produce (Ditchkoff et al. 2001; Foley et al. 2012; Jones et al. 2018), while female reproductive success is closely tied to nutritional condition (Tollefson et al. 2010; Duquette et al. 2014). Other common indices of nutritional condition in cervids include measures of body fat and body mass, as these traits are influenced by individual energetics and habitat quality (Stephenson et al. 1973; Cook et al. 2010; Tollefson et al. 2010; Ayotte et al. 2020).

As cattle competition can have direct and indirect effects on white-tailed deer nutrition, it is important to understand how this competitive relationship interacts with environmental factors to influence nutritional metrics. Soil characteristics may influence white-tailed deer habitat and forage quality (Lashley et al. 2015; Dykes et al. 2018), thereby impacting deer nutritional

condition (Stephenson et al. 1973; Cook et al. 2010; Foley et al. 2018). Research in South Texas suggests greater proportions of sand in the surface soil horizon (percent sand) can reduce forage nutritional quality, forb production, and woody species diversity (Box 1959; Ortega et al. 1997; Zhou et al. 2017; Foley et al. 2018; Fulbright et al. 2021). As such, white-tailed deer diets and nutrition may be more sensitive to cattle grazing in sandier sites, due to these forage limitations (Foley et al. 2018; Fulbright et al. 2021). Furthermore, annual rainfall and vegetational biomass production may alleviate competition between cattle and white-tailed deer, as these environmental factors are known to bolster resource availability and animal nutrition (Gordon and Illius 1989; Marshal et al. 2005; Previtali et al. 2009). Landscape structure may also influence the competitive interaction between cattle and white-tailed deer, as deer that occupy brushier landscape may be able to utilize the cover afforded by brush to avoid interacting with cattle (Loft et al. 1991; Cooper et al. 2008).

We evaluated the interactive effects of cattle competition and environmental condition on white-tailed deer nutrition by using a long-term deer capture dataset collected on working cattle ranches. We linked nutritional indices for each sex to cattle stocking rates, soil, rainfall, brush cover, and herbaceous biomass associated with georeferenced capture locations to understand how white-tailed deer nutrition was influenced by competition and environmental conditions. We developed three competing hypotheses to describe possible relationship of interspecific competition and environmental conditions on individual nutrition. We hypothesized that (1) environmental conditions will influence the effect of competition on animal nutrition and reproduction, (2) the influences of environmental condition and competition on animal nutrition are independent of each other. We predicted that greater annual rainfall, herbaceous biomass, and

brush cover and reduced percentages of sand would have positive effects on white-tailed deer nutritional condition and buffer the negative consequences of cattle competition.

Methods

Our study areas were across four South Texas ranches owned by the East Foundation: San Antonio Viejo Ranch (60,300 ha; Jim Hogg and Starr Counties), El Sauz Ranch (10,980 ha; Willacy and Kenedy Counties), Santa Rosa Ranch (7,510 ha; Kenedy County), and Buena Vista Ranch (6,120 ha; Jim Hogg County). These properties encompass 84,910 ha of native rangeland and represent a variety of ecological conditions due to gradients in abiotic factors (Figure 1.1). Annual precipitation and sand are disproportionally distributed on the South Texas landscape with coastal areas receiving greater rainfall but have sandier soils than areas farther inland (PRISM Climate Group 2021; Poggio et al. 2021). 30-year normal for rainfall in this region ranges between 50.8–71.1 cm (PRISM Climate Group 2021). Plant communities consist of live oak (*Quercus virginiana*) woodlands, thick thornscrub forest, mesquite (*Prosopis glandulosa*) savannas, and open prairies. Plants characteristic of the region include live oak, honey mesquite, huisache (*Acacia farnesiana*), brasil (*Condalia hookeri*), granjeno (*Celtis pallida*), seacoast bluestem (*Schizachyrium scoparium* var. *littorale*), purple threeawn (*Aristida woollypurea*), tanglehead (*Heteropogon contortus*), wooly croton (*Croton capitatus*), and spotted beebalm (*Monarda fruticulosa*, Montalvo et al. 2020). These properties do not allow hunting or supplemental feeding of native wildlife, limiting anthropogenic influence on the population structure and nutrition of the white-tailed deer herd providing an ideal environment to evaluate the interactive effects of environmental conditions and cattle density without the confounding effects of hunter harvest or supplemental nutrition. The East Foundation operates a cow-calf

operation on these properties and implements a rotational grazing strategy allowing for recovery of pastures after grazing by cattle.

We captured white-tailed deer at random without regard for age or sex using the helicopter net-gun method (Webb et al. 2008) annually during October and November 2017–2021. We spent one day each capturing on the Buena Vista and Santa Rosa Ranches, two days capturing on the El Sauz Ranch, and four-six days capturing on the San Antonio Viejo Ranch. Due to the size of the San Antonio Viejo Ranch, we shifted capture locations each day to ensure we were span greater variation in environmental conditions. After a deer was netted, researchers hobbled and blindfolded the deer, recorded a GPS (global positioning system) location (eTrex 10; Garmin, Olathe, KS, United States), and transported the individual via a utility terrain vehicle (UTV) to a central processing site. At this site, researchers checked for or tagged each ear of white-tailed deer with numbered steel ear tags (style 1005-49; National Band and Tag Company, Newport, KY, United States) to identify and monitor recaptures through time. Researchers then determined the age of the animal using tooth replacement and wear (Severinghaus 1949) and recorded nutritional metrics such as a modified gross Boone and Crockett antler score (ModBC; if male), lactation status (if female), body mass, and, starting in 2018, rump fat depth. Our ModBC differs from the original Boone and Crockett method (Nesbitt et al. 2009) by excluding the tip-to-tip distance of the main beams and the greatest antler spread measurement from the gross score. We measured maximum subcutaneous fat at its thickest point immediately cranial to the cranial process of the tuber ischium using ultrasonography with an Ibx Pro portable ultrasound (E.I. Medical Imaging, Loveland, CO, United States) and a 5-9 MHz linear transducer (Cook et al. 2010). After processing, researchers carried white-tailed deer approximately 25 m from the central processing station to a designated release site, where hobbles and blindfolds

were removed before the animal was released. We continuously monitored white-tailed deer vitals during processing, and all deer were handled and captured under Texas A&M University – Kingsville Institutional Animal Care and Use Committee (IACUC) permit 2020-10-19 and in accordance with the American Society of Mammologists guidelines (Sikes and Gannon 2011).

We linked the nutritional metrics of captured white-tailed deer to environmental conditions and cattle stocking rates by averaging the brush cover, herbaceous biomass, rainfall, percent sand, and stocking rates associated with the capture location. We assumed white-tailed deer were captured in the center of their home range areas and developed buffers around the capture location that approximated the sex-specific home range sizes estimated for deer in South Texas. Home range buffer sizes were 150 ha and 250 ha for females and males, respectively (Spencer et al., unpublished data; Webb et al. 2007). We sourced geospatial data for percent sand (spatial resolution: 250 m) from the International Soil Reference and Information Centre (Poggio et al. 2021), annual estimates of percent brush cover and herbaceous biomass (spatial resolution: 30 m) from the Rangeland Analysis Platform (Allred et al. 2021), and climate data related to annual rainfall totals (spatial resolution: 4 km) from the PRISM Climate Group (2021). The East Foundation provided cattle stocking data in the format of animal counts for each cattle class (Cow, Bull, Steer, Heifer) and pasture movement date records. We used these data to estimate the daily stocking densities of each pasture, from which we calculated an average annual stocking rate. Since cattle classes consume different quantities of forage depending on the age and sex of individual, we converted counts of cattle classes to equivalent animal units (AU), where cows represent 1 AU, bulls represent 1.5 AU, and steers and heifers represent 0.8 AU. We used the terra package (Hijmans et al. 2022) to create raster layers representing these stocking rates within our study areas, with a spatial resolution of 30 m. We then cycled through each