THE INFLUENCE OF FORAGE QUANTITY AND QUALITY ON THE MORPHOLOGY OF WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) IN SOUTH TEXAS

A Thesis

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ABSTRACT

The Influence of Forage Quantity and Quality on the Morphology of White-tailed Deer (*Odocoileus virginianus*) in South Texas

(May 2021)

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Historically, many ungulate sub-species boundaries were based on minor morphological differences. With the advent of molecular tools it has become apparent that most of these sub-species designations do not reflect the distribution of genetic lineages. A growing body of work has revealed that differences in body size of ungulates do follow ecoregion and soil boundaries and that these size differences are nutritionally influenced. Currently, it is unclear if these patterns of body size are a result of differences in the quantity of high-quality forage produced or from differences in nutritive value of the same plant species. I quantified differences in white-tailed deer (*Odocoileus virginianus*) body mass and antler size at 4 spatially segregated sites in South Texas, USA, using data from captured deer. I sampled forage items to determine if differences in body and antler size were best explained by forage quantity or quality. Long-term trend data, collected from 2011–2019, indicated female body mass was 9% smaller for deer captured on the eastern edge of the Coastal Sand Plain ecoregion as compared to those from the western transition zone of the Coastal Sand Plain and Tamaulipan Thornscrub ecoregions. Similarly, male body mass and antler size were 20% and 8% smaller respectively, in coastal habitats compared to more interior sites. The amount of digestible energy in browse and mast species was ~60 kcal/kg lower at sites with smaller deer body mass and antler sizes, which was about a 2% reduction in digestible energy ($\chi_3^2 = 7.40$, $P = 0.06$). Additionally, I found that the proportion of deer that had deficient levels of serum copper was greater at the site with smaller deer body mass and antler sizes (100% versus 21%, $P < 0.001$, Fisher's exact test). Overall, my research suggests that regional differences in nutritive value of primary productivity drives regional size differences in ungulate morphology.

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I. INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION[1]

Factors Affecting Phenotypic Traits in Ungulates

White-tailed deer (*Odocoileus virginianus*) are the most popular big game animal in North America (Hewitt 2011). In the U. S. alone, white-tailed deer hunting is an $87 billion dollar industry (Noble Research Institute, LLC 2018). Management of white-tailed deer in the past focused on maximizing the number of harvestable animals, but in recent decades has shifted towards creating a more balanced sex and age structure with the ultimate goal of producing desirable physical traits, (Collier and Krementz 2006, Enck and Brown 2009). Ornamentation (i.e., horns or antlers) size is generally the most important attribute to most hunters, and is therefore the focus of much research and management (Knox 2011, Harper et al. 2012). Wildlife managers use knowledge gleaned from scientific theories as a guide for population and habitat management to produce the desired population structure and physical attributes (Fulbright and Ortega-S. 2013). However, wildlife management practices can have differing, and even opposite outcomes, in different climatic, soil, and physiographic regions (DeYoung et al. 2011, Fulbright and Ortega-S. 2013, Lashley et al. 2015). Therefore, it is imperative to identify and understand the regional factors that shape phenotypic expression of physical traits (Gill 1956, Strickland and Demarais 2006, Jones et al. 2010, Lehoczki et al. 2011, Quebedeaux et al. 2019, Cain et al. 2019).

Three main factors that influence phenotypic traits of ungulates are age, genetics, and nutrition (Monteith et al. 2018, Adams 2019). Age has the largest and most predictable effect in ungulates (Monteith et al. 2009, Hewitt et al. 2014, Michel et al. 2016*a*). For example, adult

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animals are generally larger than juveniles, and reproductive output peaks at some given age for almost all individuals of a species (Hewitt et al. 2014, Newbolt et al. 2017). As a broad generalization, ungulates are long-lived species (Gaillard et al. 1998). Consequently, it takes a year, or more, for many ungulates to reach sexual maturity (Haugen 1975). Typically male cervids do not attain their maximum antler size until they are 5.5 to 7.5 years of age and after skeletal growth has ceased (Monteith et al. 2009, Hewitt et al. 2014). Age also interacts with the nutritional status of the animal. White-tailed deer in regions with poor-quality habitat often cease growth earlier than their counterparts with access to a higher plane of nutrition (Monteith et al. 2009, Fulbright and Ortega-S. 2013).

Deoxyribonucleic acid (DNA) provides the genetic code for physical traits (Watson and Crick 1953). Antler and body size of cervids are polymorphic and most likely polygenic traits (Anderson et al. 2019). By observing deer bred in captive deer facilities, it becomes apparent that it is possible to increase antler size of deer in highly controlled environments through artificial selection (Lockwood et al. 2007, Knox 2011). Heritability estimates for antlers range from 0.00 – 0.86 (Williams et al. 1994, Lukefahr and Jacobson 1998, Michel et al. 2016*a*), while estimates for heritability of body mass ranges between 0.49 – 0.64 (Williams et al. 1994, Jamieson et al. 2020). While poorly understood at this time, epigenetics certainly plays an important role in determining phenotypic expression of antler and body size in white-tailed deer (Mech et al. 1991). Research has shown that condition of the dam, and even the grandmother, of a deer will impact its antler and body size throughout its lifetime (Mech et al. 1991, Monteith et al. 2009).

Nutrition has a clear and direct impact on the phenotypic expression of physical traits (Scribner et al. 1989). To reach their genetic potential white-tailed deer must have access to high-quality forage year-round (Geist 1986), as both genotype and nutrition work together to determine phenotype (Webb et al. 2014, Foley et al. 2012). Limiting the nutrient intake of deer has negative impacts on survival, growth, and reproduction (Teer et al. 1965, Verme 1969, DePerno et al. 2000, Parker et al. 2009). Malnourished does have lowered ovulation rates, conception rates, and milk production (Teer et al. 1965, Verme 1969, DePerno et al. 2000). Lowered milk production results in increased fawn mortality and lower weaning weights (Therrien et al. 2008). Many cervids are unable to overcome the growth limitations imposed by decreased nutrition early in life, and will remain smaller than their counterparts throughout their life (Clutton-Brock et al. 1987).

Nutrient Requirements

It is clear that under-nutrition causes adverse effects in free-ranging ungulates. However, research on the specific requirements for many wildlife species is lacking. Six classes of nutrients are recognized: proteins, carbohydrates, lipids, water, minerals, and vitamins. Ungulate populations are usually limited by protein and digestible energy, which is determined by a combination of the carbohydrate, protein, lipid, and fiber content of the forage (Robbins 1993). Therefore, most research in white-tailed deer has focused on these two aspects of nutrition (Bahnak et al. 1979). Estimated maintenance needs for dietary protein and digestible energy for a non-reproductive adult white-tailed deer about 50 kg in size are 8-10% (Hewitt 2011) and 2.2 kcal/g (Hellickson and DeYoung 1997), respectively. Nutritional requirements will be elevated in response to physiological stage of the animal (Parker et al. 2009). For example, lactation, which is generally the most nutritionally demanding period for mammals, can increase the energy demands of an ungulate by as much as 215% over maintenance requirements (Oftedal 1985, Robbins 1993, Parker et al. 2009). Likewise, growing fawns have the highest protein demands, with estimated requirements of dietary protein ranging from 14 to 25% (Hewitt 2011).

The water, vitamin, and mineral requirements of white-tailed deer are largely undocumented. Minerals are used for mineralization of bones, enzyme and protein production, osmotic control, immune systems responses, and in cellular respiration. Even though we know the importance of minerals in the diet, the requirements of most wildlife species are unknown (Ammerman and Goodrich 1983). The requirements for phosphorus and sodium are well-established for white-tailed deer, but the balance of minerals with one another might be more important than the absolute value consumed in the diet (Hellgren and Pitts 1997, Grasman and Hellgren 1993). For example, it is generally recommended that the ratio of calcium to phosphorus should be close to 2:1 (Robbins 1993). Furthermore, many trace minerals interact with other minerals in complex manners (Clarkson et al. 2019). For example, copper uptake in some ruminants is hindered by other minerals, including sulfur, molybdenum, iron, and zinc (Suttle 1991). These antagonistic interactions can involve multiple minerals, such as when sulfur and molybdenum form thiomolybdates which react with copper, making it indigestible (Allen and Gawthornet 1987, Suttle 1991).

Digestive Physiology of Ruminants

Ruminants are foregut fermenters with a specialized four-chambered stomach; fermentation occurs prior to acid digestion. The symbiotic relationship with microbes allows ruminants to use the abundant, but low-quality, plant matter that is found across the world (Gibson 1968, Demment and Van Soest 1985). Through the process of fermentation, ruminants are able to digest the carbohydrate hemicellulose, which contains a β ($1 \rightarrow 4$) glycosidic bond (Gibson 1968). While fermentation allows ruminants to exploit an abundant source of energy, it is also a slow process, which places constraints upon the anatomy and diet of ruminants (Demment and Van Soest 1985, Hofmann 1989*a*). Kleiber's equation predicts that basal metabolic rate decreases with increasing body mass (Kleiber 1947). Thus, smaller animals need proportionally more energy to survive. This paradigm has led to specialization among ruminant digestive physiology. As a broad generalization, small-bodied ruminants tend to be browsers or concentrate selectors, while large-bodied ruminants are roughage or bulk feeders (Gordon and Illius 1994, Robbins et al. 1995). However, there are many exceptions to this rule. Consuming a diet that is higher quality and lower in fiber content allows these smaller-bodied ruminants to increase passage rate of food (Demment and Van Soest 1985, Wilmshurst et al. 2000). Increasing the nutrient absorption rate in this manner, enables small animals to meet their proportionally larger energy demands (Kleiber 1947, Hopcraft et al. 2012).

White-tailed deer are small-bodied ruminants and are classified as a browser or concentrate selector (Hofmann and Stewart 1972). Morphology of the white-tailed deer is typical of a browser. They have a narrow muzzle, large liver, enlarged parotid glands, and a simpler rumen with greater surface area through increased papillation, as compared to a roughage or bulk feeder (Hofmann 1988, 1989*b*; Janis and Ehrhardt 1988). Enlarged salivary glands produce more saliva, which immediately starts the chemical breakdown of nutrients, even before the food has reached the reticulorumen complex (Hofmann 1988, 1989*b*; Robbins et al. 1995). Their saliva also binds to and inactivates many plant secondary compounds, including tannins, which inhibit digestion in most animals. The rumen of a white-tailed deer is simple, in that it lacks the many folds found in a roughage or bulk feeder's rumen (Hofmann 1989*b*). The more streamlined shape of a white-tailed deer's rumen decreases the retention time of digesta (Hofmann 1988, 1989*b*). Complimentary to this is the increased papilliation in the rumen of white-tailed deer (Zimmerman et al. 2006). Having a greater surface area to volume ratio maximizes the absorption of nutrients through the rumen wall (Spilinek et al. 2020, Zimmerman et al. 2006). Altogether these adaptations facilitate quicker passage rate, and help the animal meet its energy requirements (Hofmann 1989*b*).

Foraging Behavior

The ability to use hemicellulose provides ungulates access to an abundant food source. However, forage varies in quality within and among plants and plant parts. Factors including plant phenology, species, climatic conditions, soil, and fire can influence the nutritional quality of a plant (Kuijper et al. 2009, Lashley et al. 2014, Horrell 2015, Lashley et al. 2015, Proffitt et al. 2016). For example, actively growing forbs usually contain more protein, less fiber, and are more digestible than either grasses or woody plants (Holechek 1984). Conversely, during the dormant season, non-lignified browse generally is more nutritious (Holechek 1984). Presumably all animals should forage in a manner that maximizes energy balance (Krebs et al. 1977, Pyke 1978, Senft et al. 1987). This theory has been tested explicitly in several species (Krebs et al. 1977, Pyke 1978), but there is a lack of consensus on optimal foraging in ruminants (Senft et al. 1987). Mathematical theory dictates that there is a threshold, or “giving-up” point, which will be different for each animal and landscape that dictates how selective an animal should be while foraging (Katz et al. 2015). On one end of this spectrum, a small-bodied ruminant could be ultra-selective and only eat the plants that sprouted within the past day. In this scenario, it is easy to imagine the animal starving to death while it hunts for this scarce food item. On the other end of the spectrum, our animal could eat every plant it encounters. While this strategy minimizes the time and energy spent searching for forage, it also will fill the animal’s rumen with low-quality forage that will take days to digest. Thus, foraging selectivity comes at a cost of increased foraging time, and must be balanced according to what is available on the landscape (Shipley et al. 1999, Parker et al. 2009).

Although the optimal foraging theory lacks empirical support in ungulates, there are many examples of selective feeding. For example, cattle preferentially graze in areas that have recently been burned (Augustine and Derner 2014). Heitkönig and Owen-Smith (1998) found that during the late dry season through early wet season, roan antelope (*Hippotragus equinus*) preferentially grazed on grassland swards growing on highly productive alluvial soils. These types of studies are not limited to grazers, as browsers, including white-tailed deer and roe deer (*Capreolus capreolus*), feed selectively within forest gaps (Welch et al. 1990, Reimoser and Gossow 1996, Campbell et al. 2004). Some studies have attempted to quantify the dietary niche overlap of sympatric species based on their selectivity (Schweiger et al. 2015). Unfortunately, these studies are at a very large spatial scale, and are unable to address how ungulates discriminate between individual plants and plant parts. At finer scales, studies have quantified selection of plants species and plant parts by ungulates, but the results of such studies are limited in spatial and temporal scope (Chamrad and Box 1968, Davis and Winkler 1968, Everitt and Drawe 1974, Arnold and Drawe 1979, Everitt and Gonzalez 1981, Gross et al. 1993, Martinez M. et al. 1997). Due to the intricacies and variable landscape which wild ungulates forage in, these studies only offer a brief glimpse into the foraging behavior exhibited by ungulates. To truly understand the foraging ecology of an ungulate, we need to better understand both movement patterns and the mechanisms used to determine what they ingest (Senft et al. 1987). For example, we do not know why certain plants are important in deer diets one year and then nearly non-existent in the diet the following year (Fulbright and Ortega-S. 2013). We also do not fully understand which habitat patches are perceived as useable by each species and we therefore overestimate the available forage on the landscape in many instances (Senft et al. 1987, Fulbright and Ortega-S. 2013).

Density-dependence

Most white-tailed deer management is based on density-dependent population dynamics (Collier and Krementz 2006, Enck and Brown 2009, Harper et al. 2012). The primary literature is replete with examples of large ungulate populations exhibiting density-dependent population growth. Examples include red deer (*Cervus elaphus*; Clutton-Brock et al. 1985, Borowik and Jędrzejewska 2018), mouflon (*Ovis orientalis*; Kavčić et al. 2019), guanaco (*Lama guanicoe*; Zubillaga et al. 2018) white-tailed deer (Keyser et al. 2005), bighorn sheep (*Ovis canadensis*; Douglas and Leslie, Jr. 1986), caribou (*Rangifer tarandus*; Skogland 1985), greater kudu (*Tragelaphus strepsiceros*; Owen-Smith 1990), and roe deer (Gaillard et al. 1992). While there are many different definitions of carrying capacity, the most commonly used definition is that of the nutritional carrying capacity (Macnab 1985). As the population approaches the nutritional carrying capacity, food resources become scarce due to intraspecific competition. This shortage in forage results in the heretofore mentioned negative effects caused by malnourishment (Borowik and Jędrzejewska 2018, Kavčić et al. 2019). In ungulates, juvenile animals respond more strongly to the effects of under-nutrition (Leberg and Smith 1993); populations respond first through juvenile survival and reproduction, rather than adult mortality (Gaillard et al. 1998). Furthermore, physical traits of juvenile animals are often used as sensitive indicators of diet quality. In theory, populations of ungulates never exceed the nutritional carrying capacity, but this is not always the case in actuality. Often there is a time-lag before the population responds to limited forage availability. A famous example of a population overshooting the nutritional carrying capacity, is the explosion and subsequent die-off of deer on the Kaibab Plateau in the absence of both natural and human induced predation (Leopold 1943). When ungulate populations are at or above nutritional carrying capacity, they can alter the ecosystems in which they occur, thereby influencing other species (McShea and Rappole 2000, Côté et al. 2004). Given that ungulates will have inadequate nutrition to reach their maximum size potential when the population approaches its nutritional carrying capacity, many managers keep the population below this threshold through harvest of female animals (McCullough 1999, Keyser et al. 2005).

Managing white-tailed deer populations based on density-dependent principles works throughout much of their range (McCullough 1999, Keyser et al. 2005, Harper et al. 2012). However, in some regions ungulate populations rarely reach densities high enough to exhibit density-dependent regulation (Fig. 1.1; Shea et al. 1992, DeYoung 2011). Regions with highly variable rainfall or poor-quality soils are examples of areas where population growth is generally under weak density dependence or density-independent regulation (McCullough 1999, DeYoung 2011, DeYoung et al. 2019). Shea et al. (1992) found that nutritional condition of white-tailed deer inhabiting the Florida flatwoods region, which is typified by low productivity soils, failed to respond to changes in animal density. While there is abundant forage in the form of gallberry (*Ilex glabra*) and yaupon (*Ilex vomitoria*) growing in the Florida flatwoods, it is of poor quality (Miller and Miller 1999). The copious amounts of poor-quality forage provides adequate nutrition for adult survival, but reproduction is limited (Shea et al. 1992). Similarly, in semi-arid habitats there is usually an ample amount of low- to medium-quality forage in the form of browse (Fulbright and Ortega-S. 2013). This forage base sustains adults, but, reproduction is only supported when there is a flush of growing forbs in years with above-average rainfall (DeYoung 2011, DeYoung et al 2019).

Regional Effects on Ungulate Growth

On a regional basis, trends in antler and body size of cervids often differ with soil types, vegetation communities, or both (Strickland and Demarais 2000, 2006, 2008). Studies have found that soil or physiographic region influences deer size (Gill 1956, Strickland and Demarais 2000, Jones et al. 2010, Horrell 2015, Cain et al. 2019, Quebedeaux et al. 2019). The cause is likely nutrition, as forage nutrients during early life affect growth trajectories (Michel et al. 2016*b*, Monteith et al. 2009), Soil fertility is influenced by soil composition, including nitrogen, phosphorus, potassium, organic matter, and particle size (Bridgham et al. 1996, Verhoeven et al. 1996, Van Duren and Pegtel 2000, Dykes et al. 2018). Soils with a higher percentage of clay generally have a higher cation exchange capacity and greater surface area, meaning that they retain more water and dissolved nutrients. Sandy soils tend to be prone to drought for the opposite reasons.

Total plant biomass increases with increasing soil fertility (Keddy et al. 1997, Fraser and Grimes 1998). Crude protein of deer forage plants from the southeastern U.S. varies between soil regions and might explain differences in antler and body mass between these regions (Jones 2008). Similarly, studies have documented both regional differences in mineral concentrations in white-tailed deer forage plants, and in soils (Smith et al. 1975, Jacobson 1984, Horrell 2015). Furthermore, body mass of white-tailed deer is positively correlated to soil minerals in some regions (Smith et al. 1975, Jacobson 1984). White-tailed deer will selectively forage on plants growing in more fertile soils as a result of increased nutrients in the plants (Dykes et al. 2018).

White-tailed deer are the most economically important and widespread wild ungulate in North America, and arguably the world (Hewitt 2011). Consequently, white-tailed deer may be the most-studied wild ungulate in the world (Hewitt 2011). Given this broad knowledge base and the broad geographical distribution of the species, white-tailed deer are the ideal study species to examine the influence of localized nutrition on growth and reproduction of wild ungulates (Hewitt 2011). Given their popularity as a game animal, there is a desire to understand why certain regions or areas have larger deer than other areas (Harper et al. 2012). This interest in the subject is manifested in the numerous plots of geographic variation in antler and body size of white-tailed deer (Cain et al. 2019).

The nutritional cues that lead to differences in body and antler size are not understood and may be manifested through changes in nutritional quality of plants or composition of the plant community (Gill 1956, Jones 2010, Lehoczki 2011, Cain et al. 2019, Quebedeaux et al. 2019). Currently, there are two competing hypotheses explaining how gradients in soil fertility influence white-tailed deer growth and reproduction (Lashley et al. 2015). The first hypothesis is that in areas with poor soil fertility, the quantity of forage available for deer to eat is lower (Lashley et al. 2015). For instance, the same forage species may be present, but there is less of the high-quality new growth present in sites with low soil fertility. If this is true then white-tailed deer size will still be negatively correlated with forage quantity and therefore population size in areas with non-fertile soils (McCullough 1999, Keyser et al. 2005, DeYoung 2011). Management could then manipulate white-tailed deer population size to increase the amount of high-quality forage available per individual deer (McCullough 1999, Keyser et al. 2005, DeYoung 2011). The competing hypothesis is that the nutritional content of forage plants growing in poor soils is less than that of the same plants found in more fertile soils (Shea et al. 1992). This means that deer growth is stunted in areas with poor soils as a result of forage quality rather than intraspecific competition (Jones et al. 2008, Jones et al. 2010, Lashley et al.

2015). In this scenario, fluctuations in animal density will only impact nutrient acquisition at very low densities (DeYoung 2011, Lashley et al. 2015).

Relationships between regional trends in body and antler size of white-tailed deer and nutrition have been investigated in the mesic environment of the southeastern U.S. The nutritional cues that lead to regional trends in body and antler size in semi-arid regions, where annual productivity varies with precipitation (e.g., DeYoung et al. 2019), are not well understood. In the South Texas region, high annual variation in precipitation drives recruitment, and populations rarely grow to the point where density dependence is apparent (DeYoung 2011, DeYoung et al. 2019). However, white-tailed deer antler size and body mass are inversely related to the sand content of soils (Foley, unpublished data). The purpose of my research was to determine if these regionally derived size differences in body mass and antler size are primarily driven by forage quantity or quality. Specific objectives of this research included: 1) quantify the magnitude of morphology size differences in white-tailed deer across South Texas; 2) determine if the amount of forage available explains the observed size differences in deer; 3) test if a nutrient(s) can potentially account for the observed differences in deer.

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FIGURES

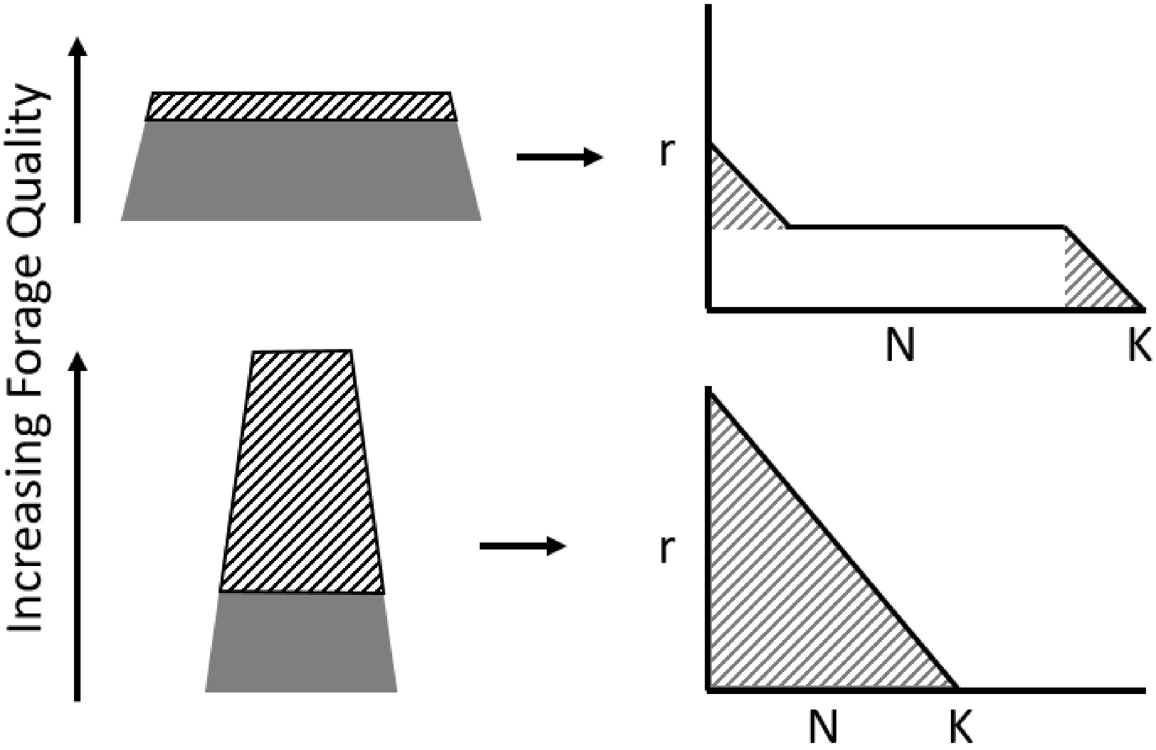

Figure 1.1. Conceptual model of ungulate population growth rates relative to differences in forage quantity and quality. Polygons on the left represent the available forage on the landscape, with the diagonal lines denoting the proportion of the total forage base with nutritional quality exceeding the level needed for subsistence (gray polygon). Corresponding graphs on the right represent the theoretical population growth that the nutritional resources will support; the Y-axis is r, or the intrinsic rate of increase, and the X-axis is N, or the number of individuals in the population. Shaded areas represent times when the population experiences density-dependent population growth and nutritional carrying capacity is denoted by K. When there is abundant high-quality forage (bottom left), intraspecific competition for food resources will result in density-dependent population dynamics across a wide range of population levels (bottom right). When there is a dearth of high-quality forage and plentiful low-quality forage, density-dependence will only be exhibited at low or high population levels (top).

II. DRIVERS OF BODY AND ANTLER SIZE IN UNGULATES ACROSS FINE-SCALE SPATIAL GRADIENTS

INTRODUCTION

The phenotype of any individual is governed by a combination of genotype and the environment. Previous work with ungulates has demonstrated that individual fitness is often positively correlated with body and ornament (i.e., antler or horn) size (Newbolt et al. 2017). Body and ornament size are genetically influenced and subject to selection, such that physical development is often assumed to be the result of "good genes" (Williams et al. 1994, Lukefahr and Jacobson 1998, Michel et al. 2016*a*, Jamieson et al. 2020). However, nutrition has a major impact on phenotypic expression of body and antler traits, and is often underappreciated (Monteith et al. 2018). Undernutrition can be caused by environmental factors, including density of conspecifics, available forage, chemical composition of forage, and efficiency of mitochondrial function (Clutton-Brock et al. 1985, Skogland 1985, Shea et al. 1992, Hill et al. 2019). Furthermore, nutrition can have multi-generational effects (Mech et al. 1991, Monteith et al. 2009, Michel et al. 2016*b*). For example, nutrition of the dam prior to parturition may have lifelong impacts on body and ornament size of offspring in ungulates (Mech et al. 1991, Monteith et al. 2009).

The prominent role of nutrition in ungulate population performance has led research and management to focus on density-dependent responses (Gaillard et al. 1998, McCullough 1999, Keyser et al. 2005, Kavčić et al. 2019). The interplay of nutrition and density-dependence on phenotypic expression in ungulates is well-known (McCullough 1999, Keyser et al. 2005). In many environments, the amount of forage available becomes limiting in the face of intra- and interspecific competition (Borowik and Jędrzejewska 2018, Kavčić et al. 2019). Based on this paradigm, one can increase individual growth and reproduction by reducing competition for forage (DeYoung et al. 2000, Harper et al. 2012).

Unfortunately, the relationship between body size and population density becomes complicated in the face of environmental stochasticity or gradients in productivity (Fig. 2.1). For instance, some ungulate populations rarely reach densities high enough to exhibit density-dependent regulation (Shea et al. 1992, DeYoung 2011, DeYoung et al. 2019). Regions with highly variable rainfall or poor-quality soils are areas where population growth is generally density-independent (Shea et al. 1992, DeYoung 2011). These areas have abundant low-quality forage that is adequate for adult maintenance, but limits reproduction and growth of juvenile animals (Shea et al. 1992, Leberg and Smith 1993, Campbell and Hewitt 2005, DeYoung 2011). Density-mediated growth and reproduction is only expressed at times of extremely low and high animal densities in such regions (Shea et al. 1992, DeYoung 2011).

At broad spatial scales, ungulate body size often co-varies with soil or vegetation communities. For instance, white-tailed deer are a broadly distributed cervid species, ranging from Canada to South America. Populations are continuously distributed throughout much of the range, yet 38 subspecies are recognized on the basis of geographic location and minor morphology differences (Heffelfinger 2011). Genetic studies indicate that the number of subspecies does not reflect the number of unique genetic lineages (Honeycutt 2000, DeYoung et al. 2003). Yet, morphological size differences are present both across and within regions, often occurring on small spatial scales. Recent research suggests that many of the morphological differences that these former sub-species were based upon may be nutritionally mediated (Strickland and Demarais 2006, Jones et al. 2010*b*, Horrell 2015, Cain et al. 2019).

At finer scales, the primary literature is replete with examples of spatial differences in body and ornamentation size in ungulates (Gill 1956, Strickland and Demarais 2006, Jones et al. 2010*b*, Lehoczki et al. 2011, Horrell 2015, Cain et al. 2019, Quebedeaux et al. 2019). Several studies have correlated regional gradients of ungulate body size with soil types (Strickland and Demarais 2006, Jones et al. 2010*b*, Lehoczki et al. 2011, Cain et al. 2019). White-tailed deer are concentrate-selectors, and must select high-quality forage to meet their energy demands (Kleiber 1947, Hofmann and Stewart 1972, Hopcraft et al. 2012). Common garden experiments have led to the hypothesis that nutritional cues result in luxury or efficiency phenotypes (Monteith et al 2009, Michel et al 2016*b*), as individuals facing nutritional limitation should invest in reproduction over skeletal growth. Nutrition is a likely driving factor behind regional trends in body size of ungulates, but the mechanism is unclear.

It is presumed that regions with more productive soils produce larger animals as a result of better nutrition, but it is unclear if productive soils produce more nutritious plants or more forage (Lashley et al. 2015). Forage quality is a function of the chemical composition of plants, and varies in response to growth stage, soil nutrients, and herbivory. As a result, the nutrient composition of plants varies greatly between functional guilds and even among species (Everitt and Gonzalez 1981). Plants assimilate nutrients from the soil into their tissues as they grow. Therefore, the mineral concentration and physical properties of soils may influence the nutritional quality of forage (Bridgham et al. 1996, Verhoeven et al. 1996, Van Duren and Pegtel 2000, Dykes et al. 2018). Previous research found that crude protein (Jones et al. 2008) and calcium (Horrell et al. 2015) content of forage increased with increasing soil productivity, which supports the forage quality hypothesis. In contrast, a separate study concluded that quantity of forage was the link between soil productivity and ungulate growth (Lashley et al. 2015). Plant diversity also has been implicated as playing a role in driving regional ungulate size differences (Strickland and Demarais 2008). The total amount of net primary productivity might be similar between regions, but the amount of useable forage will be a function of the species composition. Furthermore, eating a varied diet allows many species to minimize the negative impacts of plant secondary compounds which can be highly toxic if consumed in large quantities (Bernays et al. 1994, Singer et al. 2002). Overall, the direct link between chemical composition of forage and physical trait expression in ungulates is poorly documented and currently open to debate (Shea et al. 1992, Jones et al. 2010*b*, Lashley et al. 2015).

White-tailed deer are broadly distributed, and range from South America to Canada (Heffelfinger 2011). Deer display extensive phenotypic variation among and within regions (Gill 1956, Cain et al. 2019, Quebedeaux et al. 2019). Within regions, body mass and antler size often co-vary with spatial gradients in soil fertility (Jones et al. 2010*b*). One such region is the Coastal Sand Plain ecoregion located in South Texas, where researchers have noted that body mass and antler size is inversely related with sand content of the soil (Foley, unpublished data). It is unclear if regional ungulate size differences arise from differences in the amount of available forage, differences in the nutritive value of the same plants growing in different environments, or the diversity of forage plants that occur in different regions.

The overall goal of my research was to evaluate the hypotheses that nutrient quality or quantity may be drivers of body size differences in white-tailed deer in the south Texas region. To assess the support for these non-exclusive hypothesis regarding the underlying nutritional drivers of regional size differences in ungulates, I created *a priori* predictions on the patterns between deer size and forage quantity, nutritive value, and diversity (Table 2.1). Specifically objectives were to 1) quantify and describe size differences in body mass and antler size of white-tailed deer across the Coastal Sand Plain ecoregion in South Texas; 2) determine if the amount of high-quality forage can explain size differences in white-tailed deer morphology; 3) test if differences in nutritive value within plant species can explain gradients in white-tailed deer morphology; 4) determine if site-specific differences in forage plant diversity is related to corresponding site level white-tailed deer physical traits.

STUDY AREA

My research took place on 4 spatially unique sites located in South Texas, USA (Fig. 2.2). The El Sauz Ranch (26° 34' 42.7" N, 97° 32' 14.52" W), is located in Kenedy and Willacy Counties Texas. Willacy County received an average of 66 cm of precipitation annually and the mean yearly high and low temperature was 29.4°C and 16.7°C respectively (1981 – 2010; U.S. Climate Data 2020). The eastern border of this 10,984-ha property abutted the Gulf of Mexico. Soils belonged to the Alfisol and Entisol orders (Hines 2016). Average sand content of soils on the El Sauz Ranch were 83% (Soil Survey Staff 2020). The El Sauz Ranch encompasses three distinct ecoregions. Approximately 60% of the 10,984 ha was located on the Coastal Sand Plain, while the remainder was located on the Laguna Barrier Islands and Coastal Marshes (22%) and Lower Rio Grande Valley (19%; Omernik and Griffith 2014). Vegetation types on the site included: deep sand grasslands (52%), salty prairie (9%), deep sand live oak (*Quercus virginiana*) forest and woodland (8%), deep sand live oak shrubland (6%), active sand dune (5%), sandy mesquite (*Prosopis glandulosa*) dense shrubland (4%), wind tidal flats (3%), and sandy mesquite woodland and shrubland (3%) (Elliott et al. 2014). The remainder of the property (10%) was comprised of a mixture of 28 other vegetation types (Elliott et al. 2014). Common cacti and woody species found in the area include honey mesquite, live oak, huisache (*Vachellia farnesiana*), lime pricklyash (*Zanthoxylum fagara*), spiny hackberry (*Celtis ehrenbergiana*), brasil (*Condalia hookeri*), and toothache tree (*Zanthoxylum hirsutum*). Graminoids abundant in the area include gulf cordgrass (*Spartina spartinae*), little bluestem (*Schizachyrium scoparium*), purple threeawn (*Aristida purpurea*), and coastal sandbur (*Cenchrus spinifex*). The number of forb species native to the area was high and some of the commonly encountered species were Indian blanket (*Gaillardia pulchella*), American snoutbean (*Rhynchosia americana*), cardinal feather (*Acalypha radians*), partridge pea (*Chamaecrista fasciculata*), prostrate fleabane (*Erigeron procumbens*), sea oxeye (*Borrichia frutescens*), queen’s delight (*Stillingia sylvatica*), and crotons (*Croton* spp.).

The second site was located on the 6,123-ha Buena Vista Ranch (26° 57' 30.36" N, 98° 25' 5.16" W) in Jim Hogg County Texas. Mean annual precipitation in Jim Hogg County was 61 cm and the average annual high and low temperature was 28.9℃ and 16.0℃ respectively (1981 – 2010; U.S. Climate Data 2020). The entirety of this tract of land is located in the Coastal Sand Plain ecoregion (Omernik and Griffith 2014), which is typified by droughty soils belonging to the Alfisol order (Hines 2016). Average sand content of soils on the Buena Vista Ranch was 75% (Soil Survey Staff 2020). Predominate vegetation types were deep sand grassland (68%), sandy mesquite woodland and shrubland (28%), and sandy mesquite-evergreen woodland (3%) (Elliott et al. 2014). Honey mesquite, catclaw acacia (*Senegalia wrightii*), Texas hogplum (*Colubrina texensis*), lime pricklyash, spiny hackberry, brasil, leatherstem (*Jatropha dioica*), tasajillo (*Cylindropuntia leptocaulis*), and Texas prickly pear (*Opuntia engelmannii*) were common brush species growing in the western portion of the Coastal Sand Plain. Graminoids and forbs common to this site include, little bluestem, purple threeawn, coastal sandbur, tanglehead (*Heteropogon contortus*), hooded windmill grass (*Chloris cucullata*), red natal grass (*Melinis repens*), Indian blanket, partridge pea, Texas senna (*Chamaecrista flexuosa*), woodland sensitive pea (*Chamaecrista calycioides*), widow's tear (*Commelina erecta*), hoary milkpea (*Galactia canescens*), winecup (*Callirhoe involucrata*), and woolly croton (*Croton capitatus*).

The 2 remaining sites were located on the 60,804-ha San Antonio Viejo Ranch (26° 53' 11.45" N, 98° 47' 43.08" W) located in Jim Hogg and Starr Counties Texas. The San Antonio Viejo Ranch encompasses two ecoregions, the Coastal Sand Plain and Tamaulipan Thornscrub (Omernik and Griffith 2014), where common vegetation types included sandy mesquite woodland and shrubland (51%), deep sand grassland (37%), shallow shrubland (4%), and sandy mesquite savanna grassland (3%) (Elliott et al. 2014). Vegetation at the northern site (27° 01' 55.6" N, 98° 45' 51.9" W) was similar to that described for Buena Vista, but included thin paspalum (*Paspalum setaceum*), red lovegrass (*Eragrostis secundiflora*), hairy grama (*Bouteloua hirusta*), cenizo (*Leucophyllum frutescens*), naked Mexican hat (*Ratibida peduncularis*), doubtful Texas palafoxia (*Palafoxia texana*), and beebalm (*Monarda* spp.). Mean percent sand of soils at the northern site was 70% (Soil Survey Staff 2020). Soils at this site belong to the Alfisol order (Hines 2016), while the southern site (26° 45' 25.20" N, 98° 46' 11.90" W) has soil belonging in the Inceptisol order (Hines 2016). Percent sand content of soil at the southern site was about 55% (Soil Survey Staff 2020). The vegetation on the southern end of the San Antonio Viejo Ranch is characterized by thick brush, such as blackbrush (*Vachellia rigidula*), guayacán (*Guaiacum augustifolium*), whitebrush (*Aloysia gratissima*), guajillo (*Senegalia berlandieri*), Texas kidneywood (*Eysenhardtia texana*), leatherstem, spiny hackberry, brasil, and strawberry cactus (*Echinocereus enneacanthus*). Buffelgrass (*Pennisetum ciliare*) is dominant on the southern site, and forbs rare, but species including widow's tear can be found following episodic rain events.

All 4 of these sites are located on property owned by the East Foundation, which is a private Agricultural Research Organization that promotes the conservation of wildlife on working cattle ranches through an integrated program of ranching, science, and education (www.eastfoundation.net). As such, their landholdings are subject to periodic cattle grazing and prescribed burning as part of normal ranching activities. White-tailed deer populations on these properties are unmanaged, meaning that there is no hunting, or habitat management specifically for deer.

METHODS

Deer Morphology Data

From 2011 to 2019 white-tailed deer were captured at the 4 sites using the helicopter net-gun method (Barrett et al. 1982, Webb et al. 2008, Jacques et al. 2009). Male and female deer were captured as encountered without regard for age, sex, or physical attributes. Deer were restrained, blindfolded, and transported to a central processing site for data collection. By conducting captures in October and November each year, I minimized fluctuations in seasonal body mass change and was able to collect measurements from fully formed and mineralized antlers. I collected body mass data for both males and females to the nearest 0.45 kg using a platform scale. I quantified antler growth using the gross Boone and Crockett score (Nesbitt et al. 2009). I assigned each animal an age in 1-year increments up to 6.5 years of age, based on tooth wear and replacement (Severinghaus 1949). Aging deer using tooth replacement is highly accurate for fawns and yearlings (0.5 and 1.5 years of age), but becomes less accurate with increasing age due to the need to estimate tooth wear (Hamlin et al. 2000, Van Deelen et al. 2000, Gee et al. 2002). Therefore, I considered any deer previously captured as a fawn or yearling as known-age, and used tooth wear criteria established by Lewis (2010) for South Texas deer to estimate age of deer ≥2.5 years old.

Forage Quantity, Quality, and Diversity

Plant sampling–forb biomass. – As part of a concurrent study examining the impacts of cattle grazing on forb growth, I obtained above-ground biomass of forbs at each of the 4 study sites. Forbs represent the high-quality forage available to white-tailed deer on the landscape (Fulbright and Ortega-S. 2013, DeYoung et al. 2019). Forbs known to be avoided by white-tailed deer were excluded from the samples, following the methods of Hines (2016). Above-ground biomass samples were clipped within 50 0.25-m^2 quadrats at each of the 4 sites and dried in a forced-air oven to obtain dry matter biomass. I used data collected each autumn from 2012–2018 in my analysis.

Plant sampling–forage nutritional quality. – I collected 18 commonly encountered plant species to compare the nutritive value of the same species across sites (Table 2.2). At each of my 4 sites, I collected forage samples at 30 previously established randomly located points. I hand-plucked up to ~50 g wet weight, as available, of each species within 50 m of each point. I collected forage samples during 5 separate 2-week time periods (April 2019, late May – early June 2019, late July – early Aug. 2019, April 2020, and late May – early June 2020) to account for seasonal and yearly variation in forage nutrition. Additionally, the latter 2 time periods correspond with the third trimester of pregnancy, and peak lactation for deer in South Texas, which are 2 of the most nutritionally demanding time periods for deer. During each season, I collected samples within a 2-week period to ensure that site differences in nutrient makeup was not affected by phenological differences.

Plant sampling–diversity indices. – I obtained forage diversity indices at each of the 4 sites. I used presence-absence data for forbs consumed by white-tailed deer as delineated by Hines (2016); data were collected at 50 randomly located sites within a 2,500-ha area centered over each of the 4 sites. Forb data were collected in the Spring and Autumn during Autumn 2012 through Spring 2019 using a 0.25 m^2 quadrat. I also collected presence-absence data for all woody plants and cacti species using the line-intercept method (Canfield 1941). Transects were 50 m in length and were oriented in a previously assigned random direction in 10-degree increments. I recorded each woody plant and cactus species touching this transect. Throughout much of South Texas, brush grows in mottes or a clumped distribution across the landscape. Thus, using a large-scale sampling method (i.e., 50-m transect) as opposed to a small-scale quadrat sampling method more accurately captured the characteristics of the plant community.

Nutritional Analyses

I dried forage samples in a forced-air oven at 45°C until they reached a constant mass for 48 hrs. I ground samples to pass through a 1-mm screen using a Thomas-Wiley Laboratory Mill (Thomas Scientific, Swedesboro, New Jersey, USA). To create a composite sample for each site-species combination, I combined equal mass of processed samples. I used an independent laboratory service (Texas Research Institute for Environmental Studies, Huntsville, Texas, USA) to assay 11 minerals (calcium, copper, iron, potassium, magnesium, manganese, molybdenum, sodium, phosphorous, zinc, and sulfur) using inductively coupled plasma mass spectrometry. Additionally, I had the same laboratory service measure crude protein using the Kjeldahl method (Jurgens 2002). I determined gross energy (GE) using a Parr 6300 Bomb Calorimeter (Parr Instrument Co., Moline, Illinois, USA) for each species-site combination for one time period and used this value for all time periods, as gross energy of plants has very little temporal variation (Heaney et al. 1963, Givens et al. 1993).

Next, I performed sequential fiber analysis to estimate neutral detergent fiber (NDF) and acid detergent lignin (ADL; Goering and Van Soest 1970) using an ANKOM Technology Fiber Analysis System (Macdeon, New York, USA). I used 1 g sodium sulfite per 100 mL of NDF solution to prevent the overestimation of fiber in tannin containing forages (Hanley et al. 1992). This procedure is consistent with the Association of Official Agricultural Chemists (AOAC) guidelines, making my results comparable with other values reported in the literature (Lashley et al. 2014). Heat-stable α-amylase was used during NDF determination, following the AOAC guidelines. Previous research has shown that spiny hackberry has a high starch content (Teaschner 2006). To account for this, I used about 0.25 g of forage sample during sequential fiber analysis, rather than the standard 0.5 g, for spiny hackberry (Teaschner 2006).

I converted gross energy to digestible energy (DE) using a slightly modified approach of the equations developed by Robbins et al. (1987) and Hanley et al. (1992) for deer. The first step of this process uses the following equation to determine digestible dry matter (DDM):

$$\mathrm{DDM} = [(0.9231e^{-0.0451\mathrm{A}})(\mathrm{NDF})] + (-16.03 + 1.02\ \mathrm{NDS})$$

The NDF term in this equation is neutral detergent fiber and NDS is calculated as 100 minus NDF. The last term – A – is the lignin and cutin content expressed as a percentage of NDF and is calculated as $[(\mathrm{ADL} - \mathrm{Ash})/\mathrm{NDF}] \times 100$, where ADL is acid detergent lignin. I did not include the terms that account for tannins or biogenic silica content of monocots in the above equation. Grass consumption by white-tailed deer is generally low; therefore, most authors do not account for the decreased digestibility due to biogenic silica content (Lashley et al. 2015, Gann et al. 2019). Jones et al. (2010*a*) reported that intraspecific variation of condensed tannins in forbs collected across environmental gradients from the southeastern United States was insignificant. Once I obtained DDM, I calculated DE using the equation:

$$DE = [-0.49 + (0.99 \times DDM)/100] \times GE$$

Statistical Analyses

To quantify differences in morphology of white-tailed deer, I fitted von Bertalanffy growth curves to age specific body mass and gross Boone and Crockett scores for male and female (where applicable) deer for each of my 4 sites (Von Bertalanffy 1938, Ricker et al. 1979, Monteith et al. 2009). I compared differences in asymptotic body mass and antler sizes between sites using 95% confidence intervals calculated using the bias-corrected and accelerated (BCa) bootstrap method using 10,000 iterations.

Once I established that there were size differences in body mass and antler size of white-tailed deer between sites, I compared differences in the quantity of high-quality forage, measured as above-ground biomass of forbs eaten by deer. For this analysis I used a Friedman rank-sum test with above-ground biomass of forbs as the response variable, site as the treatment, and year as the block. A pairwise Wilcoxon rank-sum test with a Bonferroni correction was used to test for pairwise comparisons.

To test the hypothesis that nutritional quality might explain observed size differences in deer morphology across sites, I tested for differences between sites in chemical composition of plants. I split plants by guild – forbs or browse – for analysis since forbs represent a high-quality forage and browse is more of a subsistence diet (Fulbright and Ortega-S. 2013, Folks et al. 2014). Both mesquite beans and prickly pear mast were included with browse, since they are only available during the summer when deer diets include more browse and mast in South Texas. I ran a separate Friedman rank-sum test for each of 13 nutrients (digestible energy, crude protein, calcium, copper, iron, potassium, magnesium, manganese, molybdenum, sodium, phosphorus, sulfur, and zinc) for both browse and forbs. I only included a plant species in the time period average, if I was able to collect it across all sites. The southern site located on the San Antonio Viejo Ranch was not included in the forb nutritional quality analysis, as forbs were largely absent in this area. Nutrients served as the response variable, the treatments were the 4 sites, and time period when the sample was collected was the block variable. All analyses were conducted in the R programming environment (R Core Team 2020).

To determine if forage diversity could account for observed size differences of white-tailed deer between sites, I calculated a Shannon-Wiener diversity index for brush and forbs (Whittaker 1972). To calculate the Shannon-Wiener diversity index I used the equation:

$$H' = \sum_{i=1}^{n} p_i \log{(p_i)}$$

where n is species richness and p_i is the proportion of samples containing the *i*th species (Whittaker 1972). Since forbs represent a high-quality forage and browse serves as a maintenance diet in nutritionally limiting time periods, I calculated separate Shannon-Wiener diversity indices for both guilds. Since woody plant and cacti data were only available from 2019, I combined all years of forb data (2012--2019) to calculate 1 comparable diversity index for each site-guild combination. Lastly, agreement of forage quantity, nutritive values, and diversity with predictions following from deer body mass and antler trends were tabulated.

RESULTS

Deer Body Mass and Antler Size

Von Bertalanffy growth curves showed that asymptotic body mass of female white-tailed deer captured at the 2 San Antonio Viejo sites were similar, as the 95% confidence intervals overlapped and there was < 0.5 kg variation among these sites. However, body mass of white-tailed deer at the Buena Vista (44.8 ± 0.019 kg) and El Sauz (43.8 ± 0.009 kg) sites were approximately 9% smaller than the San Antonio Viejo sites (48.2 ± 0.035 kg - South, 48.5 ± 0.030 kg – North, Fig. 2.3). Male white-tailed deer at the El Sauz site only achieved an average asymptotic body mass (69.3 ± 0.052 kg) that was 82% of that observed at all other sites (Fig. 2.4). There was no statistical difference among asymptotic body mass of male white-tailed deer among the Buena Vista (84.5 ± 0.152 kg) and San Antonio Viejo North (86.8 ±1.225 kg) and South (84.4 ± 0.202 kg) sites, as the 95% confidence overlapped. While all of the 95% confidence intervals for asymptotic gross Boone and Crockett score overlapped one another, the 95% confidence intervals were wide and inspection of parameter estimates revealed large differences (Fig. 2.5). The asymptotic gross Boone and Crockett score estimate was smallest at the Buena Vista site (333.03 ± 0.638 cm) followed by the El Sauz site (334.62 ± 0.654 cm) and largest at the San Antonio Viejo sites (359.58 ± 1.580 cm - South, 360.82 ± 0.634 cm - North), resulting in an 8% difference in gross Boone and Crockett score between sites.

Forage Quantity

Above-ground biomass was highly variable between years (Fig. 2.6). After accounting for this variation we found, above-ground biomass of forbs differed between sites ($\chi_3^2 = 12.77$, $P = 0.005$). Pairwise comparisons showed that the San Antonio Viejo South site had less above-ground biomass than other sites ($P \leq 0.04$). Average above-ground biomass based on yearly data collected from 2012–2018 was 238.98 ± 147.44 kg/ha, 244.66 ± 278.36 kg/ha, 211.80 ± 163.76 kg/ha, and 24.80 ± 24.45 kg/ha for the El Sauz, Buena Vista, and San Antonio Viejo North and South sites respectively.

Nutritive Value of Forage

The sodium content in forbs differed among sites (χ_2^2 = 6.00, P = 0.05). Sodium content at the El Sauz site (0.13 ± 0.041 %) was >2 times greater than at the Buena Vista (0.06 ± 0.008 %), and at the San Antonio Viejo North (0.05 ± 0.009 %) sites. Digestible energy (χ_2^2 = 0.67, P = 0.72), crude protein (χ_2^2 = 4.67, P = 0.10), calcium (χ_2^2 = 2.00, P = 0.37), copper (χ_2^2 = 0.67, P = 0.72), iron (χ_2^2 = 0.00, P = 1.00), potassium (χ_2^2 = 4.67, P = 0.10), magnesium (χ_2^2 = 2.67, P = 0.26), manganese (χ_2^2 = 0.67, P = 0.72), molybdenum (χ_2^2 = 0.67, P = 0.72), phosphorus (χ_2^2 = 4.67, P = 0.10), sulfur (χ_2^2 = 0.00, P = 1.00), nor zinc (χ_2^2 = 2.00, P = 0.37) differed between sites in forbs (Table 2.3).

Sodium content in browse and mast differed among sites (χ_3^2 = 8.20, P = 0.05). Sodium content in sampled browse and mast was ≥3 times greater at the El Sauz site (0.18 ± 0.036 %) than at the Buena Vista (0.05 ± 0.020 %), San Antonio Viejo North (0.06 ± 0.013 %), and at the San Antonio Viejo South (0.04 ± 0.008 %) sites. Digestible energy of sampled browse and mast was approximately 2% greater at the San Antonio Viejo sites (3054.64 ± 113.12 kcal/g - North, 3,054.92 ± 161.56 kcal/g - South) as compared to the Buena Vista (2,991.49 ± 161.24 kcal/g) and El Sauz (2,996.28 ± 104.22 kcal/g) sites (χ_3^2 = 7.40, P = 0.06). Crude protein (χ_3^2 = 3.40, P = 0.33), calcium (χ_3^2 = 4.20, P = 0.24), copper (χ_3^2 = 6.60, P = 0.09), iron (χ_3^2 = 5.40, P = 0.14), potassium (χ_3^2 = 2.60, P = 0.46), magnesium (χ_3^2 = 2.20, P = 0.53), manganese (χ_3^2 = 5.00, P = 0.17), molybdenum (χ_3^2 = 3.92, P = 0.27), phosphorus (χ_3^2 = 4.20, P = 0.24), sulfur (χ_3^2 = 0.20, P = 0.98), nor zinc (χ_3^2 = 5.80, P = 0.12) differed between sites in sampled browse and mast (Table 2.4).

Diversity Indices

Shannon-Wiener diversity index values for forbs eaten by white-tailed deer were 3.89 at El Sauz, 3.67 at Buena Vista, 3.86 at the San Antonio Viejo North site, and 3.88 at the San Antonio Viejo South site. For cacti and woody species Shannon-Wiener diversity index values were 3.14 at El Sauz, 3.74 at Buena Vista, 3.64 at the San Antonio Viejo North site, and 3.80 at the San Antonio Viejo South site. Directional patterns of forage quantity, nutritive values, and diversity indices and there agreement, or lack thereof, with predicted patterns based on deer morphology can be found in Table 2.5.

DISCUSSION

Body mass and antler size of white-tailed deer differed by up to 8 to 20% within the same ecoregions in South Texas. This is in agreement with previous studies that have found gradients in soil and vegetation communities can explain regional body size and potential antler growth in ungulates (Gill 1956, Strickland and Demarais 2006, Jones et al. 2010*b*, Lehoczki et al. 2011, Horrell 2015, Cain et al. 2019, Quebedeaux et al. 2019). The smallest antler and body mass were observed on the El Sauz and Buena Vista sites, which are situated on the Coastal Sand Plain ecoregion (Omernik and Griffith 2014). The remaining sites, which had larger body mass and antler size estimates, were located at the transition zone between the Coastal Sand Plain and Tamaulipan Thornscrub ecoregions (Omernik and Griffith 2014). The Coastal Sand Plain ecoregion found in South Texas is an expansive area with sandy soils that are formed from windblown sand coming from the western edge of the Gulf of Mexico. Soils that have a high percentage of sand, such as those found within the Coastal Sand Plain ecoregion, have comparatively low soil water retention and cation exchange capacity. In times of plentiful rain, the Coastal Sand Plain ecoregion is highly productive, but due to the soils low water retention capabilities many forbs that grow in the area are ephemeral in nature (Fulbright and Ortega-S. 2013). While previous work in South Texas has shown that antler size and body mass of white-tailed deer are inversely related to sand content of the soil within the Coastal Sand Plain ecoregion, the direct nutritional link was undocumented to date (Foley, unpublished data).

Quantity of forbs differed among sites but also displayed high annual variation, probably due to variable precipitation in the south Texas region. Therefore, quantity of high-quality forage was not likely the primary driver of deer size differences on the Coastal Sand Plain. White-tailed deer attained the largest body mass and antler sizes at the 2 San Antonio Viejo sites, yet the southernmost San Antonio Viejo site had the least amount of above-ground forb production. Throughout the Coastal Sand Plain ecoregion forbs are plentiful following episodic precipitation events (Fulbright and Ortega-S. 2013). While forbs serve as a high-quality forage for white-tailed deer, they are only available during wet seasons when forage is not limiting (Campbell and Hewitt 2005, DeYoung 2011). White-tailed deer populations across South Texas rarely reach densities high enough to induce intraspecific competition for forage, and this is especially true in wet seasons when the quality and quantity of forage is greatest. Increasing the amount of a non-limiting factor (e.g., increasing available forage when forage is already plentiful) has no impact on the productivity and growth of animals.

Sodium content in sampled forbs and browse was >2 times greater on the El Sauz site where deer attain the smallest antler size and body mass, compared to the other 3 sites. Previous reports suggest that sodium is generally low in primary productivity, and is often a limiting nutrient for herbivores (Fryxell et al. 2014). Furthermore, in domestic livestock sodium only has adverse effects on growth, at extremely high levels, such as when it is purposely used to limit intake of certain types of feed (Riggs et al. 1953). Therefore, it is unlikely that the elevated sodium content in primary productivity in coastal regions explains the stunted growth of ungulates in the region. Sodium content of forage is probably an artifact of the El Sauz site's proximity to the Gulf of Mexico. While the sodium content in sampled forage does not explain the observed size differences in white-tailed deer, it does show that the mineral content of primary productivity can vary regionally. This supports the idea that subclinical mineral deficiencies can potentially drive regional differences in ungulate morphology.

Overall, my results suggest that digestible energy content of browse and mast was lower in areas where white-tailed deer attain smaller body mass and antler sizes. My findings support my hypothesis that the nutritive value of forage drives localized differences in deer body mass and antler size. This is in agreement with Splininek et al. (2020) who showed that reductions of 900 kcal/kg in digestible energy content of feed produced deer that were 5 to 10% smaller. While the magnitude of change was less for deer mass in Splininek et al. (2020), it should be noted that the authors used an eviscerated body mass rather than live body mass, which might explain this discrepancy. Herbivores often increase their intake rate in response to lowered forage quality (Meyer et al. 2010, Bonin et al. 2016). While white-tailed deer have been shown to increase feed intake when fed a low energy diet (Splininek et al. 2020), but their ability to do so is somewhat constrained as a foregut fermenter. Additionally, the intake rate of deer feeding on plants with small leaves and physical defenses, such as spines encountered on most browse species in South Texas, is potentially limited by handling time (Gross et al. 1993).

A difference of ~60 kcal/g of digestible energy might seem miniscule, but decreasing the energy intake of white-tailed deer by this amount in nutritionally demanding time periods can potentially have large impacts. White-tailed deer primarily consume browse during the summer when many forbs are senescent (Arnold, Jr. and Drawe 1979). This time period aligns with parturition and peak lactation for white-tailed deer in the area. Lactation is the single most energetically demanding time period in mammalian species (Oftedal 1985, Robbins 1993, Parker et al. 2009). The asynchronous timing of fawning and forage quality makes it necessary for white-tailed deer in this region to rely heavily on endogenous adipose stores for lactation. This results in decreased fall body condition for females that raise offspring (Rice 2018). For many ungulates in temperate and artic regions, this results in decreased overwinter survival (Monteith et al. 2013). It is unknown how this decreased body condition going into the winter impacts white-tailed deer in humid sub-tropical climates, including South Texas. In some arctic ungulates, such as caribou (*Rangifer tarandus*), the energy demands imposed by reproduction and especially lactation alters the nutritional condition of the dam and thereby can induce reproductive pauses (Cameron 1994, Gerhart et al. 1997). While this may be the case for deer in South Texas, further research is needed to substantiate this hypothesis.

Previous studies conducted in mesic environments with low variation in annual rainfall found that crude protein and calcium might explain regional size differences in body mass and antler size (Jones et al. 2008, Horrell et al. 2015). Similarly using a top down animal indicator type sampling technique, opposed to bottom up forage based method, Becker et al. (2010) suggested that minerals including calcium, copper, zinc, phosphorus, and manganese could be regionally limiting for moose (*Alces alces*) populations. Conversely, Jones et al. (2010*a*) found no evidence that plant secondary compounds, such as tannins which decrease the digestibility of forage, differed between soil regions. Using a forage, or bottom up based sampling design, I found that the digestible energy can be a regional driver of body mass and antler size differences in deer, which was previously undocumented. However, none of the other 12 nutrients that I measured followed the predict pattern necessary to explain the observed size differences in deer morphology (Tables 2.1 and 2.5). While my research was not in strict agreement as to the limiting nutrient(s) that is the underlying mechanism behind regionally derived size differences in body mass and ornamentation of ungulates, it does strengthen the overall argument that forage quality can explain spatial gradients in ungulate size.

Work published by Strickland and Demarais (2008), found that plant diversity partially explained regional size differences of white-tailed deer in forested landscapes, in the absences of agronomic crops. While my analysis on forage plant diversity was observational in nature, each of the sites with smaller deer had a 1 out of the 2 diversity indices that was lower (El Sauz – brush, Buena Vista – forbs) than the other sites. In contrast, both of the sites with larger deer had high diversity indices for both guilds of forage plants. My findings agree with those of Strickland and Demarais (2008). White-tailed deer eat highly diverse diets, which vary across both spatial and temporal scales (Berry et al. 2019, Darr et al. 2019, Gann et al. 2019). Mixing the types of forages that they consume allows herbivores to maximize nutrient intake as plant phenology changes and minimize the negative impacts of plant secondary compounds. Having a greater diversity of forage plants on the landscape theoretically makes it easier for herbivores to select a diet that can optimize nutrient uptake, while avoiding toxicities (Stephenson et al. 2006). Furthermore, having a diversity of both forbs and brush, would ensure that the nutrient demands of deer are met throughout the year, as forbs in South Texas are ephemeral in nature. Much discussion on nutrition of white-tailed deer in South Texas focuses on forbs since they represent the highest quality forage (Fulbright and Ortega-S. 2013). Yet during late summer, which is a nutritionally demanding time period for white-tailed deer, forbs are scarce and deer primarily consume browse and mast (Hewitt 2011, Fulbright and Ortega-S. 2013). The idea that regional body mass and antler size of deer are driven by floristic composition, rather than quantity or intraspecific quality of forage is intriguing, but further research is needed to test this hypothesis.

MANAGEMENT IMPLICATIONS

My research showed that there can be 8 to 20% differences in attainable body mass and antler size within small geographical areas for white-tailed deer. Quantifying the magnitude and scale of these morphological size differences allows managers and biologist to set reasonable management goals based on geographic location for trophy management of white-tailed deer. Furthermore, I found that the quantity of high-quality forage was not limiting deer growth, rather the quality of browse is possibly limiting in the Coastal Sand Plain ecoregion of South Texas. In particular, my research suggests that digestible energy in browse and mast is ~2% lower in areas with smaller deer body mass and antler sizes. I recommend wildlife managers interested in increasing body mass and antler size of deer in South Texas focus their efforts on increasing the quality and diversity, rather than the quantity, of forage.

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FIGURES AND TABLES

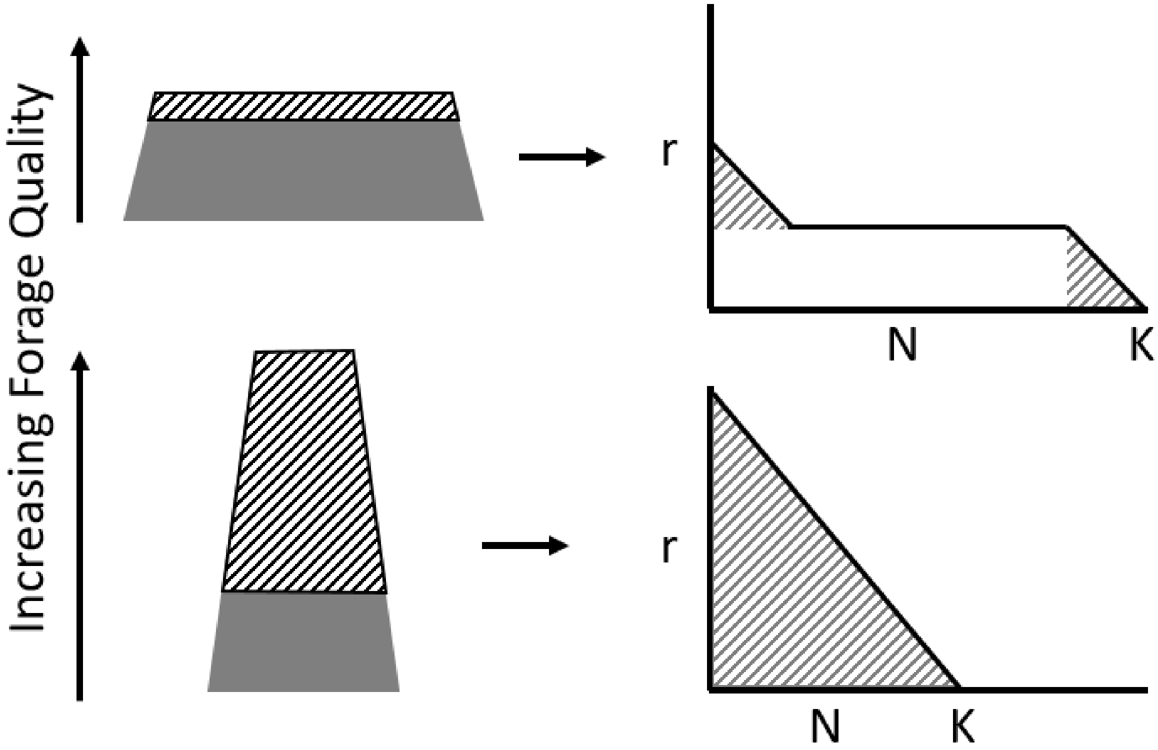

Figure 2.1. Conceptual model of ungulate population growth rates relative to differences in forage quantity and quality. Polygons on the left represent the available forage on the landscape, with the diagonal lines denoting the proportion of the total forage base with nutritional quality exceeding the level needed for subsistence (gray polygon). Corresponding graphs on the right represent the theoretical population growth that the nutritional resources will support; the Y-axis is r, or the intrinsic rate of increase, and the X-axis is N, or the number of individuals in the population. Shaded areas represent times when the population experiences density-dependent population growth and nutritional carrying capacity is denoted by K. When there is abundant high-quality forage (bottom left), intraspecific competition for food resources will result in density-dependent population dynamics across a wide range of population levels (bottom right). When there is a dearth of high-quality forage and plentiful low-quality forage, density-dependence will only be exhibited at low or high population levels (top).

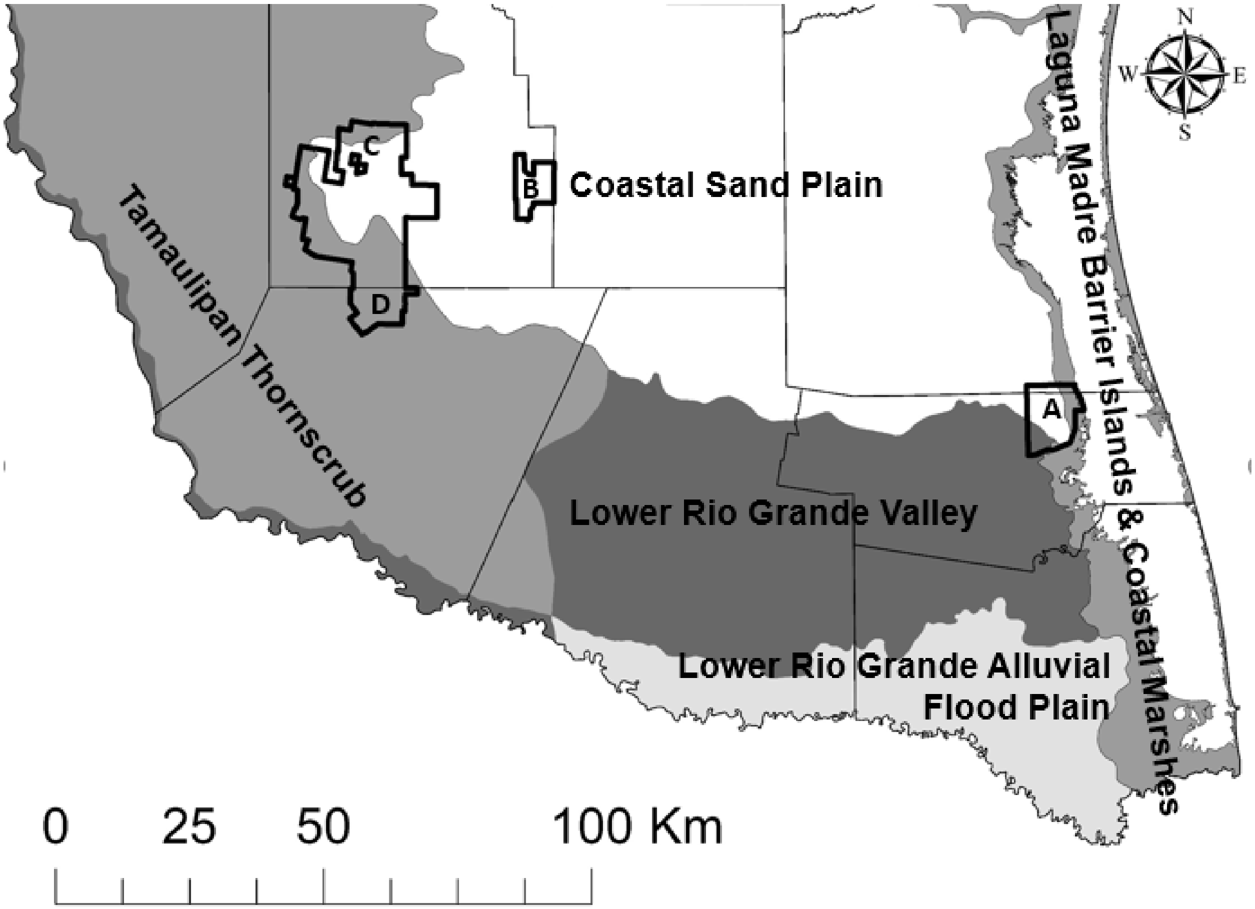

Figure 2.2. The study was conducted at 4 spatially unique sites located across the Coastal Sand Plain and Tamaulipan Thornscrub ecoregions of South Texas, USA. Sand content of soils generally decreased from the eastern to western edge of the Coastal Sand Plain ecoregion (A – El Sauz, B – Buena Vista, C – San Antonio Viejo – North, D – San Antonio Viejo – South).

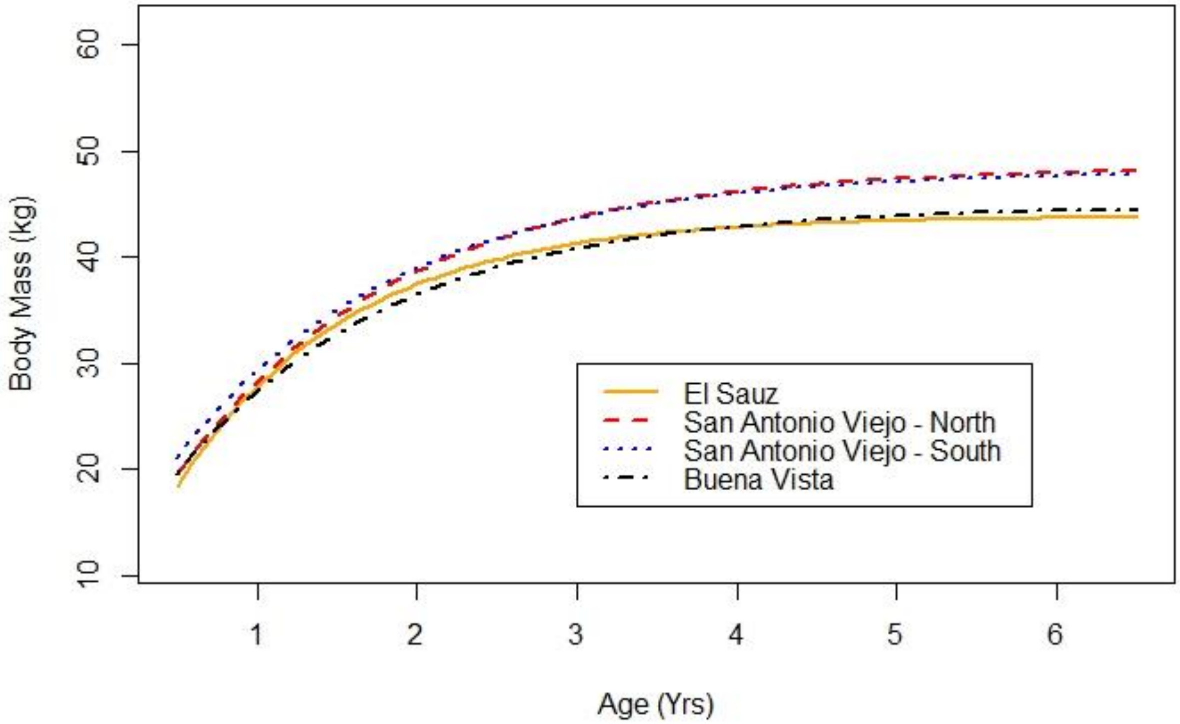

Figure 2.3. Von Bertalanffy growth curves created with age-specific body mass collected from 1,737 female white-tailed deer captured between 2011 and 2019 at 4 sites across South Texas, USA, showed that there are localized regional size differences up to 4.7 kg, which represents a 9% difference in body mass.

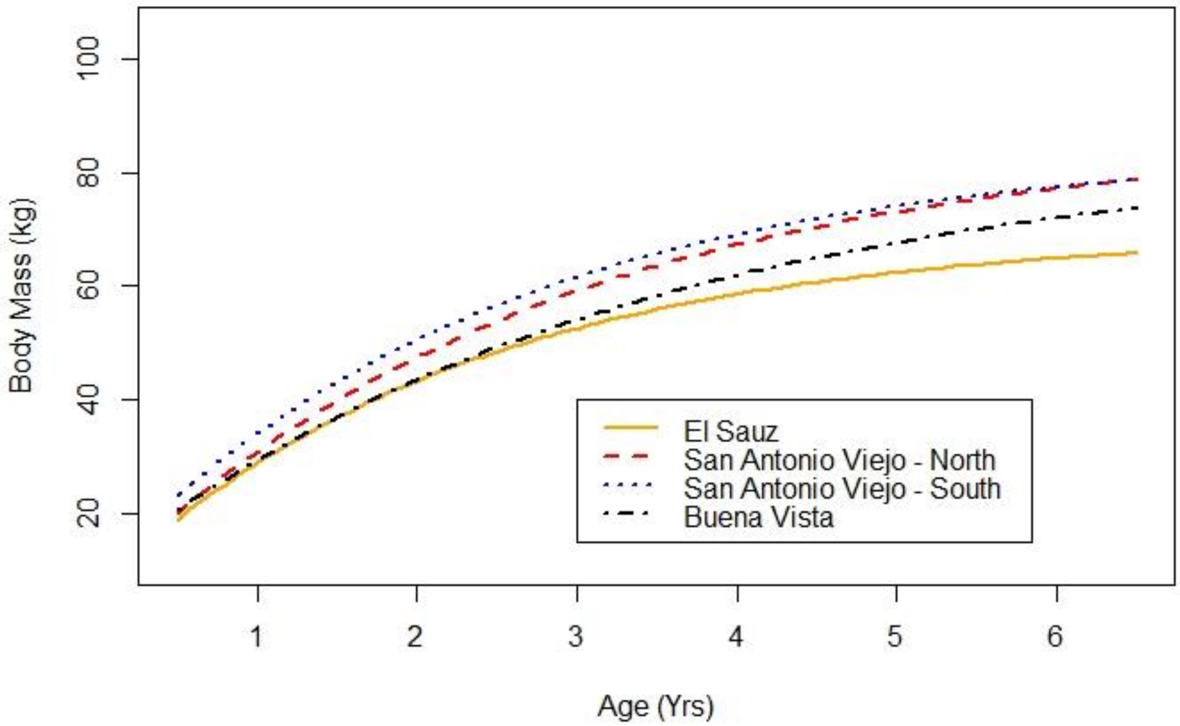

Figure 2.4. Von Bertalanffy growth curves created with age-specific body mass collected from 1,391 male white-tailed deer captured between 2011 and 2019 at 4 sites across South Texas, USA, indicated that there are localized regional size differences up to 17.5 kg, which represents a 20% difference in body mass.

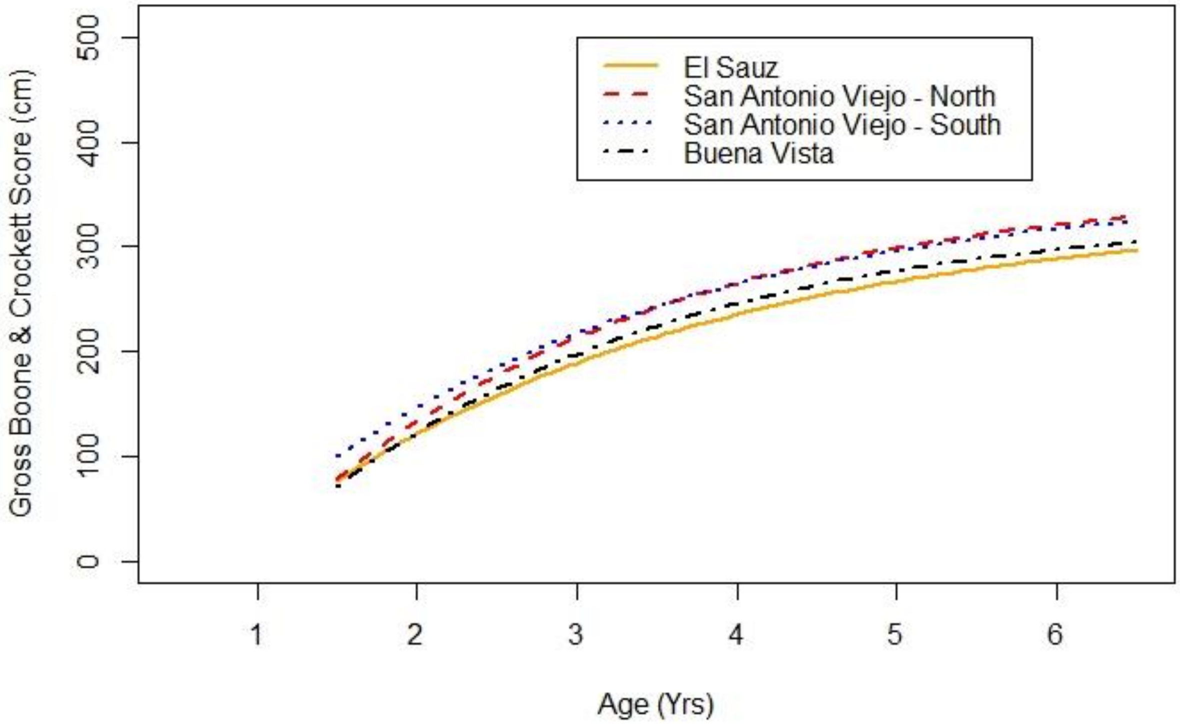

Figure 2.5. Von Bertalanffy growth curves created with age-specific gross Boone and Crockett scores collected from 1,267 male white-tailed deer captured between 2011 and 2019 at 4 sites across South Texas, USA, revealed that there are site-specific size differences up to 27.8 cm, which represents an 8% difference in antler size.

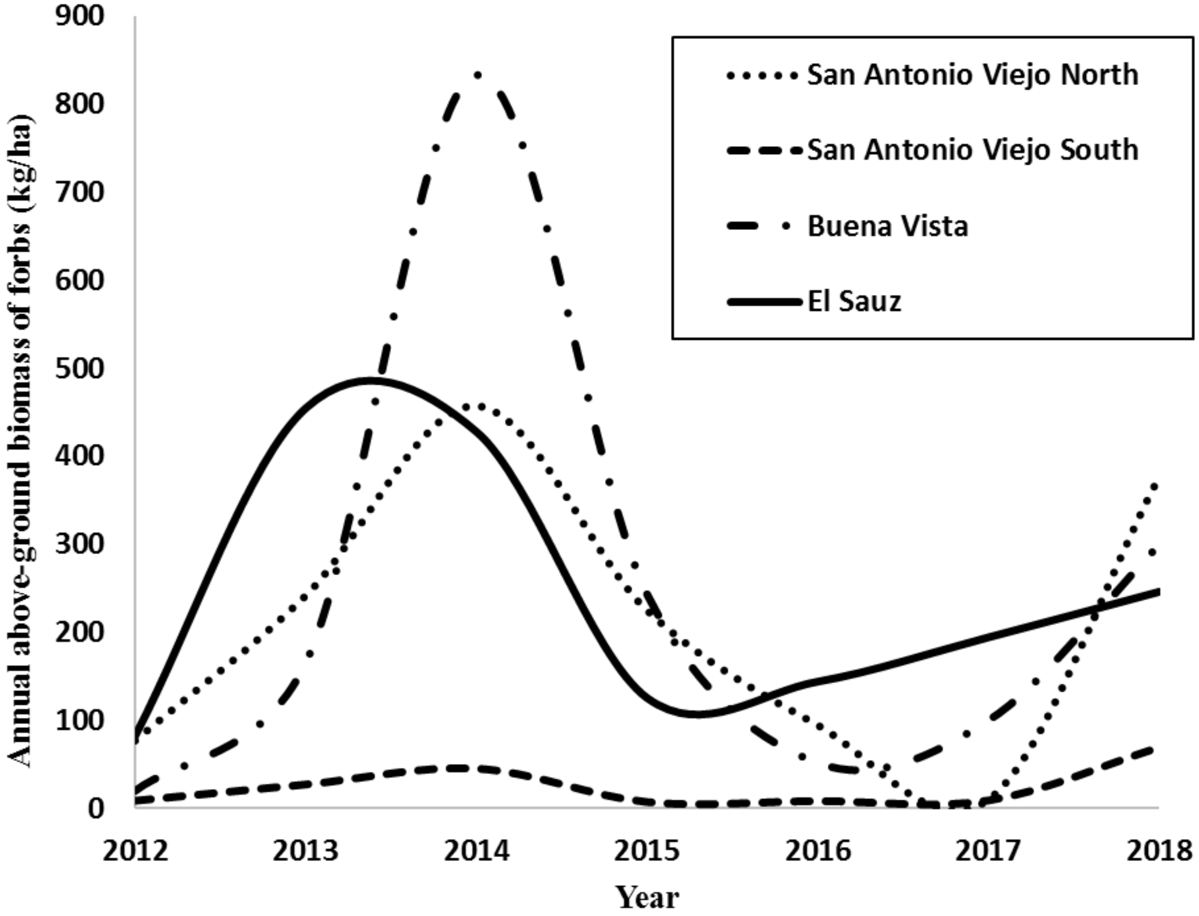

Figure 2.6. Annual above-ground biomass of forbs collected in the autumn at 4 sites in South Texas, USA, from 2012 to 2018 showed that forb production, which represent the highest quality deer forage in South Texas, is highly stochastic.

Table 2.1. Predictions for non-exclusive hypotheses pertaining to the influence of forage quantity, quality, and diversity on gradients of body mass and antler size in white-tailed deer from South Texas, USA; plus signs signify larger or greater predicted values, while negative signs indicate smaller or lesser values.

	Small-bodied Deer	Large-bodied Deer
Forage Quantity		
Above-ground biomass of forbs	−	+
Nutritive Value of Forage		
Potentially Limiting Nutrient	−	+
Potentially Toxic Nutrient	+	−
Forage Diversity		
Shannon-Weiner diversity index	−	+

Table 2.2. Plant species and parts collected for nutritional analysis from 4 sites located in South Texas, USA, during April 2019, late May – early June 2019, late July – early Aug. 2019, April 2020, and late May – early June 2020; species chosen were preferred forage plants for white-tailed deer that were present at all sites according to Hines (2016).

Scientific Name	Common Name	Part Collected
Acalypha radians	cardinal feather	whole plant
Aphanostephus spp.	lazy daisy	whole plant
Callirhoe involucrata	winecup	whole plant
Celtis ehrenbergiana	spiny hackberry	growing stem tips
Chamaecrista fasciculata	partridge pea	whole plant
Chamaecrista flexuosa	Texas senna	whole plant
Commelina erecta	widow’s tear	whole plant
Condalia hookeri	brasil	growing stem tips
Gaillardia pulchella	Indian blanket	whole plant
Opuntia engelmannii	Texas prickly pear	fruit
Prosopis glandulosa	mesquite	bean pods
Ratibida peduncularis	naked Mexican hat	whole plant
Rhynchosia americana	American snoutbean	whole plant
Richardia brasiliensis	tropical Mexican clover	whole plant
Sida lindheirmeri	Lindheimer’s sida	whole plant
Vachellia farnesiana	huisache	growing stem tips
Waltheria indica	soldier weed	leaves
Zanthoxylum fagara	lime pricklyash	growing stem tips

Table 2.3. Mean (± *SD*) nutrient content of sampled white-tailed deer forbs averaged across species, which represent the high-quality forage available to white-tailed deer, collected on 3 sites (forbs were largely absent at the San Antonio Viejo South site) in South Texas, USA, during April 2019, late May – early June 2019, late July – early Aug. 2019, April 2020, and late May – early June 2020.

Nutrient (units)	El Sauz (*n* = 54)	Buena Vista (*n* = 54)	San Antonio Viejo – North (*n* = 54)
Digestible energy (kcal/kg)	3035.69 ± 366.11	2963.94 ± 116.12	3070.94 ± 265.52
Crude protein (%)	12.55 ± 3.06	12.03 ± 3.52	12.77 ± 2.67
Calcium (%)	1.62 ± 0.18	1.87 ± 0.33	1.87 ± 0.35
Copper (ppm)	7.08 ± 2.36	7.40 ± 1.56	6.90 ± 0.89
Iron (ppm)	158.22 ± 43.35	177.19 ± 12.56	169.95 ± 48.61
Potassium (%)	1.67 ± 0.38	2.09 ± 0.26	1.86 ± 0.36
Magnesium (%)	0.36 ± 0.02	0.39 ± 0.09	0.41 ± 0.10
Manganese (ppm)	58.01 ± 4.98	64.96 ± 30.22	57.02 ± 22.75
Molybdenum (ppm)	1.11 ± 0.91	1.40 ± 1.09	1.12 ± 0.97
Sodium (%)	0.13 ± 0.04	0.06 ± 0.01	0.05 ± 0.01
Phosphorus (%)	0.16 ± 0.03	0.17 ± 0.03	0.18 ± 0.04
Sulfur (%)	0.29 ± 0.01	0.28 ± 0.02	0.29 ± 0.02
Zinc (ppm)	36.77 ± 5.66	45.47 ± 7.02	35.36 ± 10.37

Table 2.4. Mean (± *SD*) nutrient content of white-tailed deer browse and mast forage samples collected at 4 sites in South Texas, USA, during April 2019, late May – early June 2019, late July – early Aug. 2019, April 2020, and late May – early June 2020 and used as a metric of site-specific forage quality.

Nutrient (units)	El Sauz (*n* = 25)	Buena Vista (*n* = 25)	San Antonio Viejo – North (*n* = 25)	San Antonio Viejo – South (*n* = 25)
Digestible energy (kcal/kg)	2996.28 ± 104.22	2991.49 ± 161.24	3054.93 ± 113.12	3054.64 ± 161.56
Crude protein (%)	16.47 ± 5.55	15.12 ± 5.09	16.32 ± 6.07	17.15 ± 4.08
Calcium (%)	1.39 ± 0.89	1.48 ± 0.9	1.45 ± 0.78	1.64 ± 1.12
Copper (ppm)	6.76 ± 1.92	7.84 ± 2.2	7.33 ± 2.27	5.91 ± 1.07
Iron (ppm)	104.97 ± 81.4	189.67 ± 114.01	111.94 ± 63.28	123.66 ± 50.12
Potassium (%)	1.75 ± 0.68	2.16 ± 0.44	1.93 ± 0.58	2.45 ± 1.99
Magnesium (%)	0.34 ± 0.23	0.32 ± 0.15	0.33 ± 0.17	0.28 ± 0.16
Manganese (ppm)	32.88 ± 20.21	29.88 ± 12.43	28.39 ± 12.59	36.79 ± 18.77
Molybdenum (ppm)	0.84 ± 0.72	1.43 ± 1.44	1.12 ± 0.96	1.1 ± 0.73
Sodium (%)	0.18 ± 0.04	0.05 ± 0.02	0.06 ± 0.01	0.04 ± 0.01
Phosphorus (%)	0.2 ± 0.06	0.22 ± 0.06	0.23 ± 0.06	0.21 ± 0.07
Sulfur (%)	0.33 ± 0.07	0.34 ± 0.09	0.34 ± 0.04	0.32 ± 0.08
Zinc (ppm)	32 ± 16.77	40.05 ± 18.61	35.49 ± 17.82	35.04 ± 19.54

Table 2.5. Observed patterns in metrics of forage quantity, nutritive value of forage, and forage diversity at 4 sites across South Texas, USA, where size differences in body mass and antler size of white-tailed deer were observed; symbols representing the categorical rank going from smallest to largest values are: ——, —, +, and ++, and categories agreeing with predictions necessary to explain observed size differences in deer morphology are denoted with an asterisk.

	Small-bodied Deer		Large-bodied Deer	
	El Sauz	Buena Vista	San Antonio Viejo - North	San Antonio Viejo - South[1]
Forage Quantity				
Above-ground biomass of forbs	+	+	+	—
Nutritive Value of Forage				
Forbs				
Digestible energy	+	—	+	NA
Crude protein	+	—	++	NA
Calcium	—	+	+	NA
Copper	—	+	—	NA
Iron	—	++	+	NA
Potassium	—	++	+	NA
Magnesium	—	+	++	NA
Manganese	—	+	—	NA
Molybdenum	—	+	—	NA
Sodium	+	—	—	NA
Phosphorus	—	+	++	NA
Sulfur	—	—	—	NA
Zinc	—	+	—	NA
Browse and Mast				
Digestible energy*	—	—	+	+
Crude protein	—	+	+	++
Calcium	—	+	+	++
Copper	—	++	+	——
Iron	——	++	—	+
Potassium	——	+	—	++
Magnesium	+	+	+	—
Manganese	+	—	—	++
Molybdenum	—	++	+	+
Sodium	+	—	—	—
Phosphorus	——	+	++	—
Sulfur	+	++	++	—
Zinc	—	++	+	+
Forage Diversity*[2]				
Forbs	+	—	+	+
Browse and Mast	—	+	+	+

[1] Forbs were largely absent at this site and could not be included in analysis.

[2] Agreement with prediction when taken as a group (i.e. considering both groups).

III. ENVIRONMENTAL AND PHYSIOLOGICAL IMPACTS ON THE MINERAL BALANCE OF FREE-RANGING WHITE-TAILED DEER

INTRODUCTION

Minerals are critical to structural and physiological processes of animals, including mineralization of bones, enzyme and protein production, osmotic control, immune system response, and cellular respiration (Zimmerman et al. 2008, Sleeman et al. 2010, Hewitt 2011). In a biological context, minerals are usually broken into macro- and micro-, or trace minerals. Macrominerals, calcium, phosphorus, potassium, sodium, chloride, sulfur, and magnesium, are required in amounts greater than 100 mg per kg; whereas trace minerals are needed in lesser quantities. While minerals are only needed in comparatively minute quantities for bodily functioning, their importance in these roles is disproportionately larger (Hewitt 2011).

Despite the importance of minerals in the diet, the mineral requirements for most species of wildlife are poorly known (Ammerman and Goodrich 1983). There are even discrepancies in the literature on how many essential minerals there are (McDonald et al 1981, Zimmerman et al. 2008, Luna et al. 2019). Over 60 different minerals have been documented in the mammalian body, but it is unclear what, if any, purpose many minerals serve. Our overall understanding of mineral requirements in wild animals is hindered by complex interactions between minerals and environmental and physiological factors (Zimmerman et al. 2008). Many minerals interact in ways that are not fully understood (Clarkson et al. 2019). For example, copper absorption decreases in the presences of elevated levels of molybdenum and sulfur in some ruminants (Suttle 1991). Yet when molybdenum concentrations are elevated in the absence of excess sulfur, copper absorption is unaffected (Suttle 1991). In most animals, mineral requirements differ for juvenile and adults (Robbins 1993). Additionally, mineral requirements vary between sexes (Hewitt 2011). Within an age and sex class, nutrient requirements will change seasonally, as different physiological process are encountered (National Research Council 2007, Hewitt 2011).

When animals are unable to meet their nutrient requirements, it negatively impacts health. Toxicities and in some instances deficiencies of nutrients, such as starvation or grass tetany, can cause mortality. However, most deficiencies are far less dramatic and are often manifested in rough coat or hair, anemia, lowered immunity to infectious diseases and parasites, and general unthriftiness (Beldomenico et al. 2008, Zimmerman et al. 2008). Furthermore, it can be argued that every individual has experienced a subclinical nutritional deficiency at some point in their lifetime (Ceacero et al. 2015, Dykes et al. 2020). Geographical variation in mineral availability can predispose certain populations to subclinical mineral deficiencies (Sleeman et al. 2010). Some regional mineral deficiencies of ungulates are well documented and easily diagnosed from clinical symptoms, such as selenium deficiencies in California and Florida that result in lowered immune system function and decreased juvenile survival (Ros-McGauran et al. 1990, Flueck 1994, McDowell et al. 1995). However, subclinical regional mineral deficiencies can go largely undetected, given their lack of definitive symptoms (Sleeman et al. 2010, Stoklasová et al. 2019).

There is a growing body of work showing that intraspecific ungulate morphology size is correlated with soil and vegetation at a regional scale (Gill 1956, Jones et al. 2010, Lehoczki et al. 2011, Cain et al. 2019 Quebedeaux et al. 2019). These regional size differences in ungulate morphology are thought to be nutritionally mediated, but the direct link with forage composition is largely undocumented at this time. Much research on regional differences in ungulate body and ornament size focuses on macronutrients, even though a common symptom of mineral deficiencies is retarded growth. This is not altogether surprising, as there is a paucity of information on diagnosing mineral deficiencies in wildlife.

To accurately diagnose mineral imbalances in an animal, it is important to have well-established baseline values from healthy individuals for the tissue being tested (Schultz et al. 1994, Zimmerman et al. 2008). White-tailed deer are one the most geographically widespread species of wild ungulates, and probably the most-studied wild ungulate species in the world (Hewitt 2011). However, many of the mineral requirements of white-tailed deer are undocumented and the impact and implications of regional subclinical mineral deficiencies is currently unknown. Several case-studies that have examined clinical symptoms of selenium deficiency in ungulates (Ros-McGauran et al. 1990, Flueck 1994, McDowell et al. 1995). Baseline hepatic mineral concentrations of white-tailed deer are limited (Schultz et al. 1994, Zimmerman et al. 2008, Sleeman et al. 2010). Given the broad geographic range and diversity of habitats inhabited by white-tailed deer, it is unlikely that the full range of normal values for healthy individuals has been captured in these reports (Zimmerman et al. 2008, Sleeman et al. 2010). It is also unclear if regional deficiencies can account for reported size differences between soil regions. Given the lack of definitive baseline mineral values for white-tailed deer, managers and veterinarians usually rely on values from domestic livestock (Zimmerman et al. 2008, Sleeman et al. 2010, Hewitt 2011).

The best method for assessing the mineral status of an individual involves using hepatic mineral concentrations (Roug et al. 2015, Zimmerman et al. 2008). The liver plays a role in detoxification and serves as a storage reservoir for many minerals (Kincaid 1999). As such, mineral concentrations in the liver are highly sensitive to fluctuations in mineral acquisition and can be used as an accurate reflection of short-term mineral balance (Kincaid 1999).

Unfortunately, this process is highly invasive and is usually collected post-mortem (Roug et al. 2015, Stoklasová et al. 2019). Whole blood or serum are the most commonly sampled tissues to ascertain the mineral health of a live specimen, (Stoklasová et al. 2019). Even though serum and whole blood are currently the best alternatives to liver samples, they are not perfect indicators of mineral status in live animals (Roug et al. 2015). For example, manganese and copper concentrations are only weakly correlated with hepatic concentrations at best (Vermunt and West 1994, Roug et al. 2015). Iron serum concentrations usually are quite stable, given its importance in oxygen transport, and therefore is only useful for assessing iron stores when bodily iron reserves reach very low levels (Matrone et al. 1947). Blood samples can be collected from live animals, but to do so requires sedation or capture and restraint of the animal. Other tissues, such as hair and antler, can potentially be collected passively (e.g., hair snares and shed antlers) helping to reduce the cost of monitoring wildlife populations. Furthermore, different tissues reflect distinct temporal scales and can be used to answer questions regarding seasonality of mineral deficiencies in animals (Kincaid 1999).

The goal of my study was to further our knowledge on the impacts of mineral health on free-ranging populations of Cervids and the interrelationship between the abiotic environment and nutrition of wild Cervids. Specific objectives were to 1) assess the usefulness of hair and antler as a less invasive procedure to determine the mineral status of free-ranging white-tailed deer; 2) explore the physiological and environmental factors that might predispose Cervids to mineral aberrations; and 3) determine if morphological size differences of deer between sites can be explained by mineral deficiencies and how this is related to the mineral concentrations of soil and primary productivity.

STUDY AREA

My study took place on two spatially segregated sites in South Texas (Fig. 3.1). The first of my 2 sites, the El Sauz site, is located in Willacy and Kenedy Counties, Texas, USA (26° 34' 42.7" N, 97° 32' 14.52" W). The eastern border of the El Sauz site borders the Gulf of Mexico. Mean annual precipitation in Willacy County was 66 cm; average annual high and low temperatures were 29.4℃ and 16.7℃, respectively (1981 – 2010; U.S. Climate Data 2020). El Sauz is located at the confluence of 3 level IV ecoregions (Omernik and Griffith 2014). Approximately 60% of the 10,984 ha is on the Coastal Sand Plain, while the remainder is located on the Laguna Barrier Islands and Coastal Marshes (22%) and Lower Rio Grande Valley (19%; Omernik and Griffith 2014). Regional vegetation types commonly encountered on the El Sauz site included deep sand grasslands (52%), salty prairie (9%), deep sand live oak (*Quercus virginiana*) forest and woodland (8%), deep sand live oak shrubland (6%), active sand dune (5%), sandy mesquite (*Prosopis glandulosa*) dense shrubland (4%), wind tidal flats (3%), and sandy mesquite woodland and shrubland (3%; Elliott et al. 2014). The El Sauz site has soils belonging to the Alfisol and Entisol orders (Hines 2016). Woody species, including live oak, honey mesquite, huisache (*Vachellia farnesiana*), lime pricklyash (*Zanthoxylum fagara*), spiny hackberry (*Celtis ehrenbergiana*), brasil (*Condalia hookeri*), toothache tree (*Zanthoxylum hirsutum*), and Texas persimmon (*Diospyros texana*), grow in mottes scattered throughout the area. Common plants growing in open areas included gulf cordgrass (*Spartina spartinae*), little bluestem (*Schizachyrium scoparium*), purple threeawn (*Aristida purpurea*), coastal sandbur (*Cenchrus spinifex*), Indian blanket (*Gaillardia pulchella*), American snoutbean (*Rhynchosia americana*), cardinal feather (*Acalypha radians*), partridge pea (*Chamaecrista fasciculata*), prostrate fleabane

(*Erigeron procumbens*), sea oxeye (*Borrichia frutescens*), queen's delight (*Stillingia sylvatica*), and crotons (*Croton* spp.).

The second site, the Coloraditas Grazing Research and Demonstration Area (hereafter Coloraditas) is located in Jim Hogg County, Texas, USA (27° 01' 55.6" N, 98° 45' 51.9" W). Mean annual precipitation in Jim Hogg County was 61 cm, and the average annual high and low temperatures were 28.9℃ and 16.0℃ respectively (1981 – 2010; U.S. Climate Data 2020). The Coloraditas site is comprised of 7,502 ha of native rangeland located on the transition zone between the Coastal Sand Plain and Texas-Tamaulipan Thornscrub level IV ecoregions (Omernik and Griffith 2014, Montalvo et al. 2020). Most soils found on the Coloraditas site belong to Alfisol order (Hines 2016). Common regional vegetation types found on the Coloraditas site were deep sand grassland, sandy mesquite woodland and shrubland (Elliott et al. 2014). Woody species, including honey mesquite, catclaw acacia (*Senegalia wrightii*), Texas hogplum (*Colubrina texensis*), spiny hackberry, brasil, leatherstem (*Jatropha dioica*), and cenizo (*Leucophyllum frutescens*), grew scattered throughout the area. Texas prickly pear (*Opuntia engelmannii*) and tasajillo (*Cylindropuntia leptocaulis*) were also common across the Coloraditas site. Open areas were dominated by a mixture of grasses and forbs, including purple threeawn (*Aristida purpurea*), coastal sandbur (*Cenchrus spinifex*), tanglehead (*Heteropogon contortus*), red lovegrass (*Eragrostis secundiflora*), hairy grama (*Bouteloua hirusta*), hooded windmill grass (*Chloris cucullata*), Indian blanket, partridge pea, Texas senna (*Chamaecrista flexuosa*), woodland sensitive pea (*Chamaecrista calycioides*), widow's tear (*Commelina erecta*), hoary milkpea (*Galactia canescens*), winecup (*Callirhoe involucrata*), woolly croton (*Croton capitatus*), naked Mexican hat (*Ratibida peduncularis*), doubtful Texas palafoxia (*Palafoxia texana*), and beebalm (*Monarda* spp.).

Both of these properties are owned by the East Foundation, which is a private Agricultural Research Organization that promotes the conservation of wildlife on working cattle ranches through an integrated program of ranching, science, and education (www.eastfoundation.net). The landholdings are subject to periodic cattle grazing and prescribed burning as part of normal ranching activities. Populations of native mammals inhabiting the properties owned by the East Foundation were not subject to hunting or management. Wildlife on the properties were not supplemented through feeding or baiting and were reliant on naturally occurring vegetation for nutritional homeostasis.

METHODS

Deer Capture and Data Collection

As part of a long-term study on East Foundation lands, scientists from Texas A&M University-Kingsville captured white-tailed deer during 2011 to 2019 using the helicopter net-gun method (Barrett et al. 1982, Webb et al. 2008, Jacques et al. 2009). Deer were captured as encountered without regard for age or sex; all deer were restrained, blindfolded, and transported to a central processing site for data collection. By conducting captures in October and November each year, I minimized fluctuations in seasonal body mass change and was able to collect measurements from fully formed and mineralized antlers. I assigned each animal an age in 1-year increments up to ≥6.5 years of age, based on tooth wear and replacement (Severinghaus 1949). Additionally, I recorded the lactation status of female deer, as lactation is the most nutritionally demanding physiological process for mammals. I collected age-specific morphology measurements to quantify differences in antler size, body mass, and skeletal size. I quantified antler growth using the gross Boone and Crockett score (Nesbitt et al. 2009), and hind foot length, measured from the top of the keratinized hoof to the posterior end of the tuber calcis, as an index of skeletal size of deer. All animals were weighed using a platform scale to the nearest 0.45 kg.

Twenty mL of blood was drawn from the jugular vein of each deer. I centrifuged blood at approximately 3,500 rpm until serum and red blood cells separated. Then I pipetted blood serum into a cryogenic vial and froze the serum at -20 C until analysis. A hair sample was collected from the rump area using a pair of electric clippers and an antler sample was collected from male deer using anvil loppers. Antler samples consisted of the distal 2.54 to 4 cm of the main beam. I stored hair and antler samples at room temperature until analysis.

Forage and Soil Sample Collection

Soil samples were collected and tested for each of my 2 sites as part of a concurrent study (Drabek, unpublished data). Soil samples were collected at 49 (Coloraditas) and 43 (El Sauz) randomly located points within a 2,500 ha circle that roughly corresponded to deer capture locations, using standard sampling procedures (Hines 2016, Drabek, unpublished data).

At 30 randomly located points within the same 2,500 ha circle, I collected 14 different deer forage plants that are ubiquitous within the Coastal Sand Sheet ecoregion of Texas (Hines 2016). Species I collected were American snoutbean, Lindheimer's sida (*Sida lindheirmeri*), brasil (growing stem tips and leaves), cardinal feather, huisache (growing stem tips and leaves), Indian blanket, lazy daisy (*Aphanostephus* spp.), honey mesquite (bean pods), partridge pea, naked Mexican hat, tropical Mexican clover (*Richardia brasiliensis*), Texas prickly pear (mast), soldier weed (*Waltheria indica*), and widow's tear. I hand-plucked about 50 g wet weight of each species within a 50-m radius of the randomly located point as available. I collected forage samples during 5 separate 2-week time periods (April 2019, late May – early June 2019, late July – early Aug. 2019, April 2020, and late May – early June 2020) to account for seasonal and yearly variation in forage nutrition. During each season, I collected samples within a 2-week period to ensure that site differences in nutrient makeup was not masked by phenological differences. Forage samples were dried in a forced-air oven (~45°C) until they reached a constant mass for 48 hrs. I ground samples to pass through a 1-mm screen using a Thomas-Wiley Laboratory Mill (Thomas Scientific, Swedesboro, New Jersey, USA).

Sample Preparation and Mineral Analysis

I selected a subset of tissue (serum, antler, and hair) samples to have analyzed for mineral content, such that my sample would include 1 deer from each age-sex class (0.5 - 6.5+ yrs. in 1 yr. increments for both females and males) from each site, for a total of 28 deer. To account for the potential confounding effect of year, I selected a subset of samples from the same year (2015) to use for analysis. I used a cordless drill mounted rasp to powder antler samples prior to chemical digestion. Hair and serum samples required no prior preparation. To create a composite forage sample for each site-species combination, I combined equal mass of processed forage samples. I used an independent laboratory (Texas Research Institute for Environmental Studies, Huntsville, Texas, USA) to measure concentrations of 11 minerals in hair, antler, and forage samples and 10 minerals in serum samples with inductively coupled plasma mass spectrometry. A second laboratory service (Texas AgriLife Extension Soil Testing Laboratory, College Station, Texas, USA) was contracted to quantify concentrations of 10 minerals in soil samples. Minerals of interest included calcium, copper, iron, potassium, magnesium, manganese, molybdenum, phosphorous, sodium, sulfur, and zinc, as these minerals are considered important in the health of domestic ruminants and are routinely tested in livestock feeds (Ammerman and Goodrich 1983, Luna et al. 2019). Molybdenum was not measured in serum or soil. Molybdenum levels would have been undetectable in serum (R. Smith, Texas

Research Institute for Environmental Studies, personal communication). Soil samples were collected as part of a concurrent study in which molybdenum concentrations were not analyzed and was therefore unavailable.

Statistical Analysis

Assessment of less invasive sampling. – To test if hair and antler tissue serve as a good alternative to using serum for determining the mineral balance of white-tailed deer I tested for correlation of minerals between serum and hair, serum and antler, and hair and antler. If mineral levels in ≥2 tissues were correlated, it would indicate that the mineral concentration in the tissue(s) varied with the amount available in the animal in a predictable manner, making it useful for diagnostics. I first tested for bivariate normality using a Royston test (Royston 1992). Since my data lacked bivariate normality, I used a non-parametric Spearman's rank correlation to test for correlations.

Physiological and environmental factors. – To quantify mineral levels for deer inhabiting native South Texas rangelands, I calculated means and standard deviations for each mineral and tissue combination for males and females separately. I also calculated means and standard deviations for serum mineral concentrations of all deer by site. Lastly, I calculated means and standard deviations for serum mineral values for lactating and non-lactating females ≥1.5 yrs. of age. To place my results in context of existing reference values, I compared individual values to the reference values for cattle (*Bos* spp.) as listed in Puls (1981) and Puls (1994; as reported by Creekmore and Glaser 1999). While the values published by Puls (1981, 1994) are from domestic ruminants (i.e. cattle, sheep and goats), they are routinely used as the baseline values for *Odocoileus* species and have even been wrongly cited as actually coming from deer (Creekmore and Glaser 1999, Zimmerman et al. 2008, Sleeman et al. 2010). This shows that these are currently the most widely accepted reference values for white-tailed deer. I converted all reference values to ppm for ease of comparison. Proportions of sampled deer with serum mineral values outside of the published normal range were calculated for each mineral. Additionally, I calculated the average number of mineral abnormalities (those values outside of the published normal range) based on serology on an individual deer basis. I used Fisher's exact tests (Fisher 1934) to test if the proportion of females ≥1.5 yrs. of age with serum mineral abnormalities differed as a function of lactation status.

Site-level size differences and soil and primary productivity. – The long-term capture records indicate that deer are consistently smaller at the El Sauz than the Coloraditas site. Presumably this difference is nutritionally mediated (Rice 2018, Chapter 2). To establish the magnitude of these size differences, I fitted a separate von Bertalanffy growth curve for body mass, hind foot length, and antler score (gross Boone and Crockett score; males only) for male and female deer at the El Sauz and Coloraditas sites using age-specific morphometric measurements collected between 2011 and 2019 (Von Bertalanffy 1938, Ricker et al. 1979, Monteith et al. 2009). Aging deer using tooth wear and replacement is highly accurate for fawns and yearlings (0.5 and 1.5 years of age), but becomes less accurate with increasing age (Hamlin et al. 2000, Van Deelen et al. 2000, Gee et al. 2002). Therefore, I corrected estimated age of any deer previously captured as a fawn or yearling, determined by the presences of uniquely number ear tags, to improve accuracy of ages for this analysis. Once I had created von Bertalanffy growth curves, I computed the asymptotic size differences, as a percentage, between sites for each metric and sex. I compared differences in asymptotic body mass, hind foot length, and antler sizes between sites using 95% confidence intervals calculated using the bias-corrected and accelerated (BCa) bootstrap method using 10,000 iterations. I used Fisher's exact tests (Fisher

1934) to test if the proportion of animals that had mineral abnormalities based on serology differed between sites (El Sauz or Coloraditas).

To test for differences between sites in soil mineral concentrations I used a Welch's *t*-test as the data exhibited heteroscedasticity, signified by a Levene's test (Levene 1960). I used a paired *t*-test to test for differences in forage mineral concentrations between sites. Forage mineral data violated the assumption of within-group normality, and numerous transformation methods were tested, but failed to improve the distribution. Yet, the assumption of homogenous errors of the variance was met, as indicated by a Levene's test (Levene 1960). The *t*-test is quite robust to violations of normality within groups, as long as the samples meet the assumptions of equal errors of the variance and independence (Ratcliffe 1968, Sawilowsky and Blair 1992, Sawilowsky and Hillman 1992). Thus, I deemed it was acceptable to still use the parametric *t*-test in this situation. All statistical tests were performed in the R computing environment (R Core Team 2020), with the aid of the car (Fox and Weisberg 2019), MASS (Venables and Ripley 2002), and MVN (Korkmaz et al. 2014) packages.

RESULTS

Assessment of Less Invasive Sampling

I found that potassium concentrations were positively correlated between serum and hair (t_{25} = 4.30, r_s = 0.65, $P < 0.001$), serum and antler (t_9 = 2.31, r_s = 0.61, $P = 0.05$), and hair and antler (t_9 = 2.88, r_s = 0.69, $P = 0.02$). Calcium concentrations of hair and antler were negatively correlated (t_9 = 2.66, r_s = -0.66, $P = 0.03$). The other 24 element-tissue combinations tested were not statistically significant at an $\alpha = 0.05$ level (Table 3.1). Given my specified alpha level for these statistical tests, 1.4 individual tests were expected to be statistically significant due to chance out of the 28 Spearman’s rank correlation tests run. Mineral concentrations were greatest in antler and hair samples, and lowest in serum samples (Table 3.2).

Physiological and Environmental Factors

All 28 deer tested had ≥5 serum mineral values (Table 3.3) that are considered deficient or above normal. On average, each deer had 6.3 (out of 10) minerals that were above normal or deficient. Zinc and copper were deficient in all or some individuals, while all other abnormalities were above the reported normal range for these elements. I was unable to find previously reported values for normal serum chemistry pertaining to sulfur. Zinc serum levels were deficient for 100% of the deer tested. Likewise, 100% of the deer tested had iron, magnesium and phosphorus levels greater than the reported normal ranges. Potassium levels were above the normal reference value for 25% of tested deer. For sodium, manganese, and calcium, 96%, 4%, and 4% of the sampled deer had higher than normal values, respectively. Copper values were deficient in 61% of the animals, with remaining 39% of the sampled deer falling on the other end of the spectrum with values that were higher than normal reported ranges. All 5 lactating females ≥1.5 yrs. of age had serum copper levels that were deficient (Table 3.4). Conversely, 3 out of 7 (43%) of non-lactating females ≥1.5 yrs. of age had serum copper deficiencies. This difference in proportion of animals with serum copper deficiencies between lactating and non-lactating animals was marginally not statistically significant (P = 0.08, Fisher’s exact test). The proportion of serum mineral abnormalities did not differ between lactating and non-lactating females ≥1.5 yrs. of age for any other minerals ($P \geq 0.42$, Fisher’s exact test).

Site-level Size Differences and Soil and Primary Productivity

Asymptotic body mass and hind foot length, for both females and males, were statistically different as shown by non-overlapping 95% confidence intervals. Asymptotic body mass of female deer at the Coloraditas (48.5 kg; 47.52–49.57 95% CI) site was 9% larger than the El Sauz (43.8 kg; 43.35–44.31 95% CI) site (Fig. 3.2 and Table 3.5). Hind foot asymptotic length was 3% and 4% greater at the Coloraditas (female 36.23 cm; 36.07–36.40 95% CI; male 38.88 cm; 38.71–39.03 95% CI) site as compared to the El Sauz (female 35.21 cm; 35.10–35.32 95% CI; male 37.38 cm; 37.21–37.56 95% CI) site for female and male deer respectively. Male deer achieved an asymptotic body mass that was 20% greater at the Coloraditas (body mass 86.8 kg; 82.78–91.66 95% CI; antler size 360.82 cm; 342.77–390.52 95% CI) site and asymptotic antler scores that were 8% greater than the El Sauz (body mass 69.3 kg; 67.28–71.88 95% CI; antler size 334.62 cm; 310.99–373.16 95% CI) site (Fig. 3.3). However, the 95% confidence intervals for antler sizes overlapped.

All 14 deer (100%) captured at the coastal El Sauz site had deficient copper serum levels, while only 21% (3 of 14) of the animals caught at the Coloraditas site were deficient ($P < 0.001$, Fisher's exact test, Table 3.3). No other serum mineral abnormalities differed between sites ($P = 0.08$, Fisher's exact test). Of the 3 animals caught on the Coloraditas site that had deficient serum copper levels, 2 were lactating females and 1 was a male fawn.

Soil calcium concentrations were 2.6 times higher at the El Sauz site ($\bar{x} = 1117.12 \pm 2065.49$ ppm) than at the Coloraditas site ($\bar{x} = 434.98 \pm 88.58$ ppm, $t_{42.14} = 2.16$, $P = 0.04$, Table 3.6). There was a statistically significant difference in soil copper concentrations between the El Sauz ($\bar{x} = 0.27 \pm 0.27$ ppm) and Coloraditas ($\bar{x} = 0.14 \pm 0.05$ ppm) sites ($t_{44.82} = 2.16$, $P = 0.003$). Iron soil concentrations were 2 times greater at the El Sauz site ($\bar{x} = 8.53 \pm 6.23$ ppm) than at the

Coloraditas site ($\bar{x}$ = 4.18 ±1.87 ppm, $t_{48.62}$ = 4.41, $P < 0.001$). Magnesium soil concentrations were 3 times greater at the El Sauz site ($\bar{x}$ = 243.07 ±297.76 ppm) than at the Coloraditas site ($\bar{x}$ = 81.78 ±19.31 ppm, $t_{42.31}$ = 3.55, $P < 0.001$). Manganese soil concentrations were 1.3 times greater at the Coloraditas site ($\bar{x}$ = 9.23 ±2.79 ppm) than at the El Sauz site ($\bar{x}$ = 7.29 ±4.20 ppm, $t_{71.55}$ = 2.57, $P = 0.01$). Sodium soil concentrations were 101 times greater at the El Sauz site ($\bar{x}$ = 211.82 ±444.69 ppm) than at the Coloraditas site ($\bar{x}$ = 2.10 ±1.00 ppm, t_{42} = 3.09, $P = 0.003$). There were no other statistically significant differences in soil mineral concentrations between sites ($P \geq 0.27$, Table 3.7). Sodium concentrations in collected forage plants were 2.8 times greater at the El Sauz ($\bar{x}$ = 0.14 ±0.13 %) than the Coloraditas site ($\bar{x}$ = 0.05 ±0.06 %, t_{56} = 4.72, $P < 0.001$, Table 3.6). There were no other statistically significant differences in forage mineral concentrations between sites ($P \geq 0.08$, Table 3.7).

DISCUSSION

When assessing the mineral status of ruminants the most reliable and accepted method involves testing a piece of liver (Zimmerman et al. 2008). Unfortunately, using hepatic mineral concentrations is highly invasive and can only be collected post-mortem (Roug et al. 2015, Stoklasová et al. 2019). Serum and whole blood have been used successfully to monitor the mineral balance of live animals (Matrone et al. 1947, Roug et al. 2015, Stoklasová et al. 2019). For this method to be useful it is necessary to have a range of normal mineral concentration collected from healthy animals to compare our results to (Zimmerman et al. 2008). Even when there are published ranges for the species of interest, using whole blood and serum for mineral testing poses problems. The liver is a detoxifying organ, meaning that excess mineral in the body will accumulate in it. Conversely, blood is used to transport nutrients throughout the body, and therefore certain elements are highly regulated. For example, iron plays an essential role in the enzyme hemoglobin which is used to transport oxygen (Matrone et al. 1947). Other metals measured in serum, including copper and manganese, are weakly correlated to hepatic level making it hard to compare levels between substrates (Vermunt and West 1994, Roug et al. 2015). Therefore, having high levels of these minerals in the serum might not necessarily be linked to toxicity, as minerals in the bloodstream are more tightly regulated than those in the liver. Yet, when a mineral deficiency is observed in serum it theoretically is a good indicator that the body has an inadequate supply of the element in question, since non-essential stores should be depleted before essential stores. This idea is supported by my observation that apparently healthy deer had ≥4 minerals that were at abnormally high levels. Furthermore, research from numerous Bovids from Africa and domestic livestock have shown that related species often have different mineral requirements and responses (Drevemo et al. 1974, Puls 1981). Therefore, mineral reference values will differ between species and regions for many animals. While we only sampled deer from a single year, it seems more plausible that our current knowledge regarding what actual serum mineral ranges are is incomplete, rather than randomly capturing 28 animals that all were suffering from multiple mineral imbalances.

Serum and whole blood are considered the best option when testing for mineral toxicities and deficiencies in live ungulates (Roug et al. 2015, Stoklasová et al. 2019). The ability to use other body tissues, such as antler and hair, to accurately determine the mineral health of free-ranging white-tailed deer has several benefits (Stoklasová et al. 2019). The collection of blood samples, requires the capture and restraint of animals. In many wildlife species, the capture and restraint of animals often involves the use of chemical sedation. Previous reports suggest that chemical sedation can impact the serology of ungulates (Smith 2011). The ability to determine the mineral health of wild ungulates using a biological sample that can be passively collected without capture (e.g., hair snares and shed antlers) would alleviate these concerns (Stoklasová et al. 2019). Furthermore, having multiple methods to test for mineral deficiencies and toxicities in animals, would allow managers, veterinarians, and scientists to compare results from multiple methods making their final conclusions more robust.

Hair has previously been suggested as a substitute to serum and whole blood (Dunnett and Lees 2003, Asano et al. 2005, Roug et al. 2015, Stoklasová et al. 2019). The efficacy of using mineral concentrations in hair varies with species and mineral (Combs 1987, Roug et al. 2015, Stoklasová et al. 2019). In the past, hair has been used to assess mineral balance in livestock, horses (*Equus ferus*), eland (*Taurotragus derbianus*), moose (*Alces alces*), mule deer, and white-tailed deer (Franzmann et al. 1977, Combs 1987, Jones and Weeks, Jr. 1998, Jones 2002, Dunnett and Lees 2003, Asano et al. 2005, Becker et al. 2010, Roug et. al 2015, Stoklasová et al. 2019). Even though hair has been previously used in research, the feasibility of using hair as an indicator of mineral status of white-tailed deer was previously untested (Jones and Weeks, Jr. 1998, Jones 2002). Ideally, to use hair and antler to determine mineral status of an animal, the mineral concentrations should be positively correlated with another substrate or have established baselines for both healthy and clinically deficient animals. This would indicate that as more of the mineral is consumed by the animal, more of the mineral is also deposited in the tissue. My results indicate that neither hair nor antler mineral concentrations are correlated with other tissues mineral concentrations, suggesting that it is unwise to use hair or antler as a substitute for the standards of liver and blood without more accurate reference values. This conclusion agrees with the general idea that hair is a poor indicator of mineral balance in most mammals. However, hair and antler still have the potential to provide information on mineral uptake by animals over different temporal scales than serum and liver samples, if accurate reference values for the species in question are established. For example, white-tailed deer usually grow antlers over a 5-6 month time span. Yet mineralization of antlers usually occurs in a couple week time span and is often reliant on endogenous mineral stores. To accurately use antler and hair to assess mineral balance in white-tailed deer, there is a need for further research to establish what ranges for deer exhibiting clinical signs of deficiencies and toxicities are for these tissues, as all of my samples were collected from apparently healthy deer. Based on my findings, I suggest that research centered upon hair mineral levels should be carefully scrutinized before accepting the results.

The fact that all deer that I tested exhibited multiple serological mineral abnormalities suggests that our current knowledge of acceptable ranges is incomplete. With the exception of copper, all minerals tested were unidirectional as far as abnormalities go. For example, all 28 deer were deficient in zinc and had above-normal levels of iron, magnesium, and phosphorus according to previously reported norms (Puls 1981, 1994, see Table 3.3). In extreme cases deficiencies and toxicities of these minerals can lead to severe symptoms, but under most circumstances the primary symptoms are decreased feed intake, and lowered growth and fitness (Puls 1981). It is also important to remember that all deer tested were apparently healthy individuals. While there has been some information pertaining to normal serological mineral values in white-tailed deer published, it is limited in scope and often based on a small sample size of individuals (Weeks, Jr. and Kirkpatrick 1976, Seal et al. 1981, DelGiudice et al. 1987, DeLiberto 1989, DelGiudice et al. 1992, Smith 2011). My research shows that healthy animals have more variation in serum mineral values than was previously documented.

Long-term trends on age-specific body mass, antler size, and skeletal size show that deer on the El Sauz site are smaller than deer inhabiting the Coloraditas site. Previous work suggests that these observed size differences are nutritionally mediated (Rice 2018, Chapter 2). Observational studies cannot prove causality, but the fact that all 14 deer tested from the El Sauz site had deficient serum copper levels that were 90% lower than deer from the Coloraditas site on average suggests that copper might be a limiting deer growth coastal habitats. Copper is a component of several oxidative enzymes, including ceruloplasmin, metallothionein, lysyl oxidase, superoxide dismutase, and cytochrome c oxidase (Minate and Carfagnini 2002, Ayub et al. 2013). Hypocuprosis in ruminants can results in elongated hoofs, swollen joints, hind limb weakness, diarrhea, enteritis, enzootic ataxia, rough coat and hair growth, retained placentas, suppressed immune system response, and convulsions (Zimmerman et al. 2008, Sleeman et al. 2010, Ayub et al. 2013). Copper also is involved in regulating heart rate, and in extreme cases deficiencies can result in heart failure (Ayub et al. 2013). More often, copper deficiencies in wild ungulates results in suppressed growth, lowered reproductive output, and increases the animal's risk to secondary factors, such as predation and infectious diseases (Sleeman et al. 2010). It has also been suggested that copper balance might play a role in chronic wasting disease (CWD) infections in Cervids (Zimmerman et al 2008, Nichols et al. 2016), but other research seems to refute this idea (Wolfe et al. 2010, 2020).

Ruminants can experience either primary or secondary hypocuprosis (Spears 2003). Primary copper deficiencies are caused by inadequate copper supply in forage. For domestic cattle, 10 ppm of dietary copper is sufficient (National Research Council 2007). Secondary deficiencies are a result of lowered copper absorption in the digestive tract. In general, ruminants are bad at assimilating dietary copper (Spears 2003). Copper absorption in forages can vary seasonally, as dietary copper absorption is lowered in phenologically young forage, which has a low fiber and high crude protein content (Blakley et al. 2000). Interactions between trace minerals also hinders absorption of copper in ruminants (Spears 2003). The most important interaction occurs among copper, molybdenum, and sulfur (Dick 1953). In the presence of elevated sulfur and molybdenum levels, monothiomolybdates, dithiomolybdates, trithiomolybdates, and tetrathiomolybdates are formed (Gooneratne et al. 1989, Suttle 1991). These thiomolybdates react with copper to form insoluble complexes that are indigestible (Allen and Gawthornet 1987). Therefore, optimal diets for cattle should have a copper to molybdenum ratio around 6:1 as ratios ≤ 2:1 routinely cause hypocuprosis (Miltimore and Mason 1971). Additionally, elevated levels of dietary sulfur can result in the formation of copper sulfide in the digestive tract, which reduces the absorption of copper (Suttle 1974). High levels of iron consumption has also been shown to reduce the hepatic copper stores in adult cattle and sheep (Bremner et al. 1987, Prabowo et al. 1988). Zinc is another trace mineral implicated in secondary copper deficiency in ruminants. Presumably, the observed hypocuprosis in white-tailed deer was caused by the low levels (~ 7 ppm) of copper in tested forage plants, as the copper to molybdenum ratio exceeded the recommendation of 6:1 (National Research Council 2007). However, it should be noted that there was no difference in copper, molybdenum, and sulfur in tested forages between sites even though copper deficiencies in the tested deer was site dependent. This discrepancy highlights our imperfect knowledge of trace mineral nutrition in wild ungulates.

Regional differences in soils and vegetation communities often drive intraspecific size differences in wild ruminants. McNaughton (1990) found that fine-scale geographical variation in soil and forage mineral content drives habitat selection and migratory behavior in some ungulates. However, for non-migratory ungulates, fine-scale differences in soil and forage mineral availability can predispose regional populations of ungulates to trace mineral deficiencies or toxicities (Sleeman et al. 2010). Under ordinary circumstances these nutritional stressors have minimal impact on population-level persistence (Fielder 1986). Yet, it is important to understand regional differences in wild ruminant mineral health, as the lowered productivity as a result of imbalances can be the difference between population persistence and extinction for species of conservation concern or in the presence of novel pathogens and predators (Chihuailaf et al. 2014). While previous research has shown that animal mineral balance is influenced by the soil and plant mineral concentrations (Jones and Weeks, Jr. 1998, Jones 2002, Ayub et al. 2013), my results do not show this same relationship. All deer tested at the coastal El Sauz site were deficient in copper and deer from the interior Coloraditas site, with the exception of 1 fawn and lactating individuals, had high concentrations of serum copper. Yet, the copper concentrations in the soil at the El Sauz site were approximately double the concentration of copper at the Coloraditas site. Additionally, there was no evidence these differences are being caused by secondary copper deficiency, since there was no difference in sulfur and molybdenum concentration in the forage collected from the 2 sites. I did not detect a difference in copper concentrations within the forage plants sampled, but this does not necessarily mean that dietary copper was the same for deer at both sites. It has been shown that different classes of forage have differing copper concentrations (Paterson et al. 1999). Furthermore, deer consume a highly diverse diet and the floral composition of deer diets between sites might account for the discrepancy between animal and forage copper levels (Folks et al. 2014, Darr et al. 2019, Gann et al. 2019).

Young ruminants obtain most of their copper stores in utero, as most species' milk has a low copper content (Rombach et al. 2002). Therefore, late gestation is thought to deplete copper reserves (Wirth and Linder 1985). The copper content of milk certainly varies with copper status of the individual, but copper is usually not a mineral that receives much attention as being limiting during lactation (Rombach et al. 2002). The observation that all 5 lactating females I tested were experiencing hypocuprosis based on serum copper concentrations suggests otherwise. Site-level effects (3 lactating individuals were from the El Sauz site) and small sample size could be alternative explanations for this trend. Yet, Salem (2017) found that lactating domestic sheep and goats had decreased copper serum levels as compared to non-lactating individuals in a controlled environment. This indicates that copper might play a larger role in lactation in small ruminants than previously thought.

MANAGEMENT IMPLICATIONS

My research shows that many of the normal serum mineral ranges used for diagnosing deficiencies and toxicities are incomplete and are inaccurate for white-tailed deer from some, if not most, regions of their range. Values obtained from my research will aid mangers, researchers, and veterinarians interested in assessing trace mineral health in free-ranging ruminants. Furthermore, I found that copper is possibly limiting growth of ruminants in coastal habitats bordering the Gulf of Mexico. Copper deficiencies in my study were strongly site based, and may explain regional body mass and antler size differences of white-tailed deer. While I discovered many mineral abnormalities based on serum reference values, they were generally ubiquitous across sites and most likely are a result of imperfect knowledge, rather than actual mineral abnormalities. Based on my research, I believe providing access to a supplemental source of copper in these regions can increase the productivity of wild ruminant populations.

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FIGURES AND TABLES

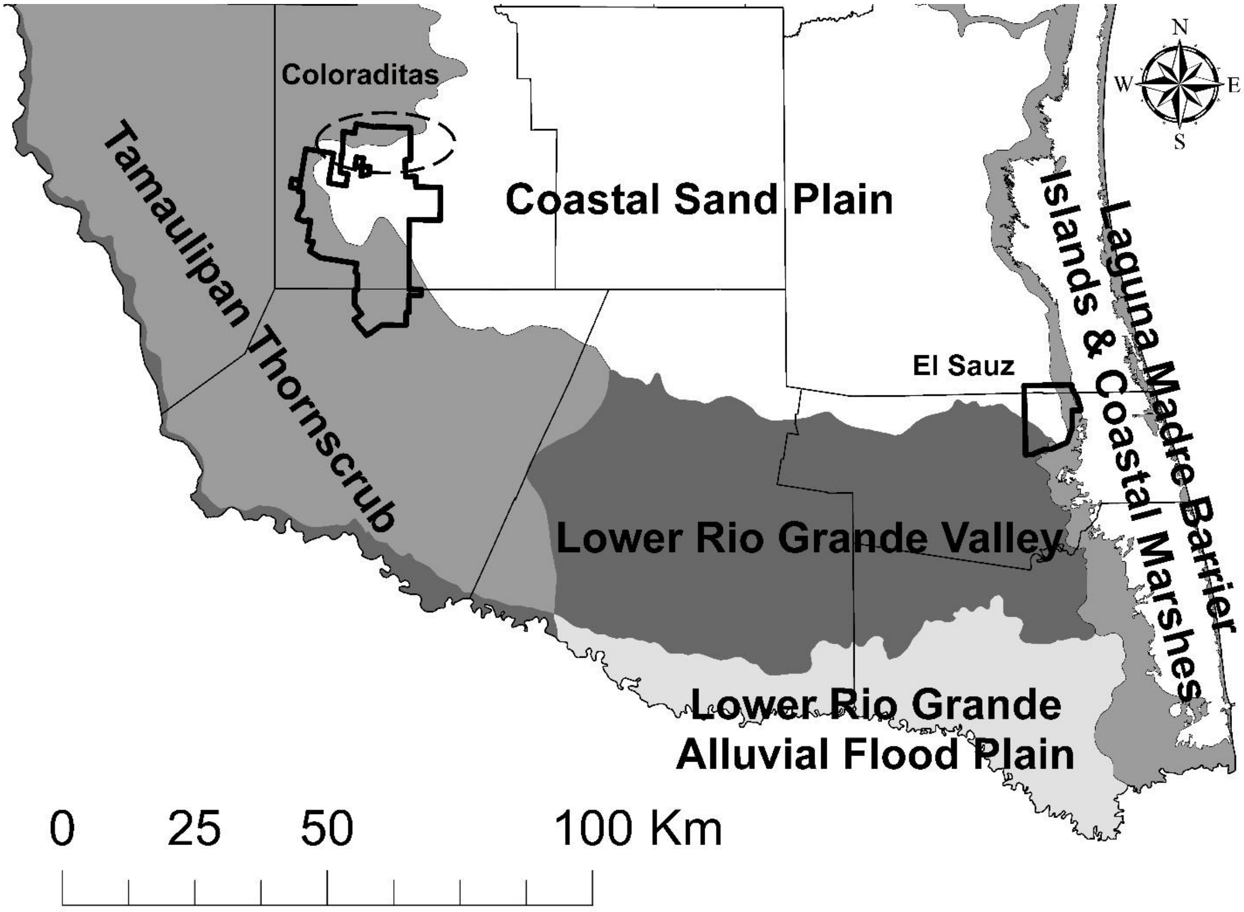

Figure 3.1. The El Sauz Ranch and the interior Coloraditas Grazing Research and Demonstration Area, located in South Texas, USA. The El Sauz site is primarily situated on the Coastal Sand Plain ecoregion and has sandier soils than the Coloraditas site which is located on the western boundary of the Coastal Sand Plain.

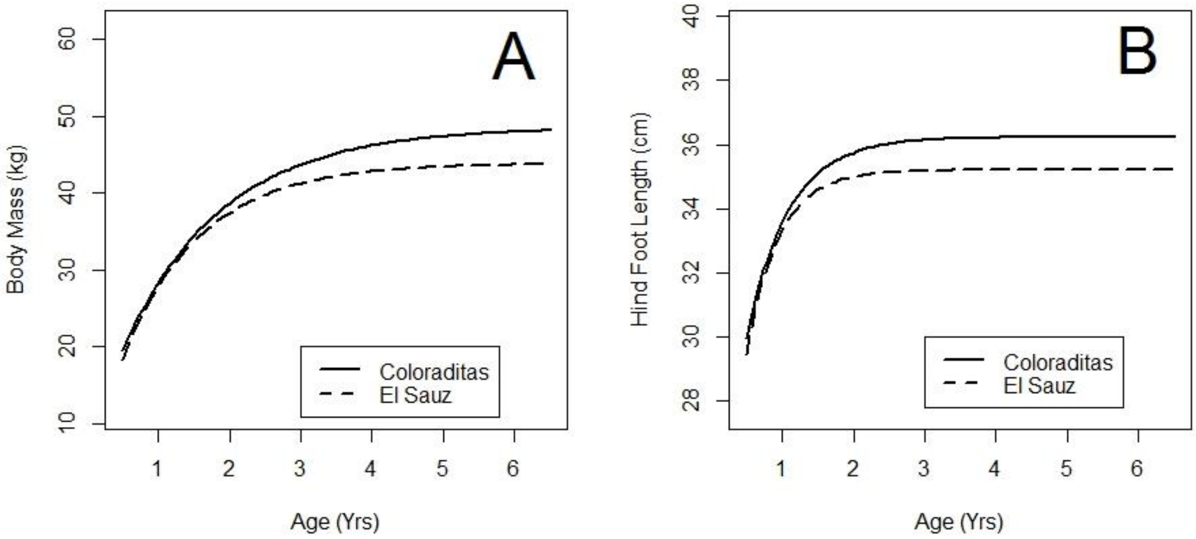

Figure 3.2. Von Bertalanffy growth curves constructed with morphology measurements collected from female white-tailed deer captured annually between 2011 and 2019 showed mean asymptotic body mass (kg; A) and hind foot length (cm; B) at the Coloraditas site were 9% and 3% larger than those from the El Sauz site, respectively. These differences represent long-term regional differences, rather than yearly perturbations in morphological size differences of white-tailed deer in South Texas, USA.

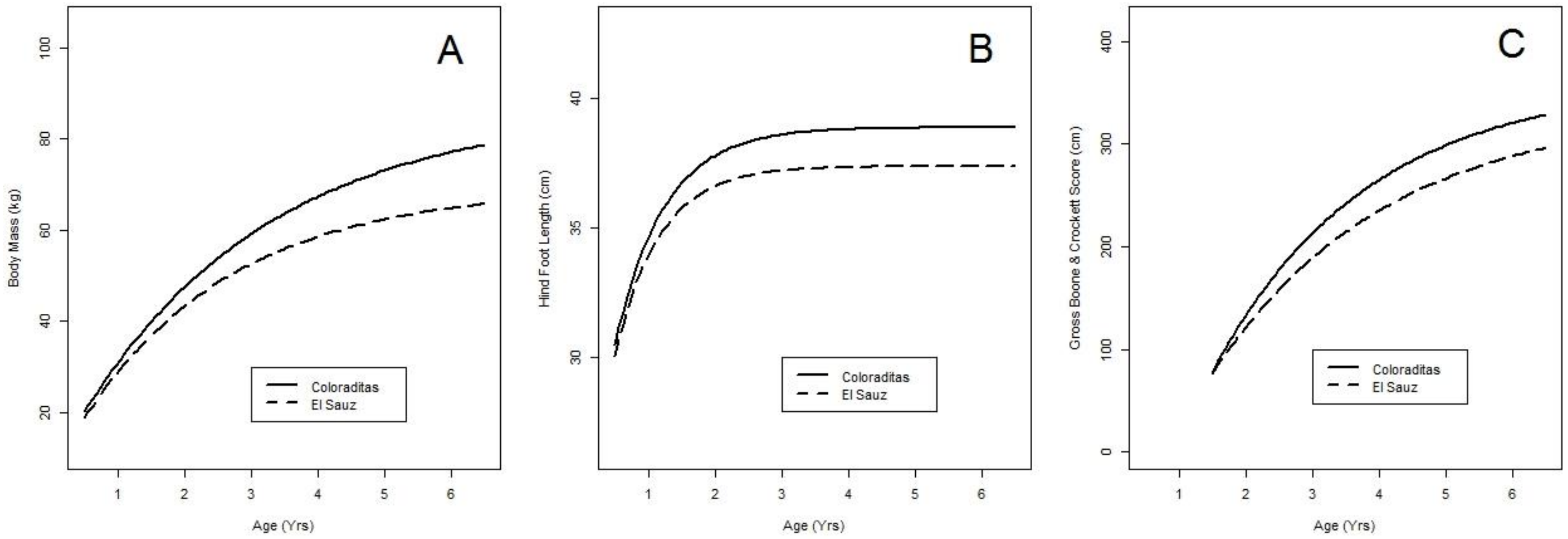

Figure 3.3. Von Bertalanffy growth curves constructed with morphology measurements collected from male white-tailed deer captured annually between 2011 and 2019 showed mean asymptotic body mass (kg; A), hind foot length (cm; B), and antler score (cm; C) at the Coloraditas site were 20%, 4%, and 8% larger than those from the El Sauz site, respectively. These differences represent long-term regional differences, rather than yearly perturbations in morphological size differences of white-tailed deer in South Texas, USA.

Table 3.1. Spearman rank correlations among serum, hair, and antler for 11 different minerals, measured in tissue samples collected from white-tailed deer in South Texas, USA, during October and November, 2015.

Mineral	Serum and Hair (n = 27)			Serum and Antler (n = 11)			Hair and Antler (n = 11)		
	r_s	$t_{(25)}$	*P-value*	r_s	$t_{(9)}$	*P-value*	r_s	$t_{(9)}$	*P-value*
Ca	0.1	0.51	0.61	0.05	0.14	0.89	-0.66	2.66	0.03
Cu	0.01	0.07	0.94	-0.46	1.54	0.16	-0.47	1.61	0.14
Fe	0.04	0.2	0.84	-0.28	0.88	0.4	0.09	0.26	0.8
K	0.65	4.3	0.0002	0.61	2.31	0.05	0.69	2.88	0.02
Mg	-0.004	0.02	0.98	0.21	0.63	0.54	0.01	0.03	0.98
Mn[1]	0.24	1.23	0.23	-	-	-	-0.1	0.29	0.78
Mo[1]	-	-	-	-	-	-	0.36	1.17	0.27
Na	0.08	0.42	0.68	-0.51	1.79	0.11	0.55	2	0.08
P	0.2	1.01	0.32	0.05	0.16	0.88	-0.55	1.98	0.08
Zn[1]	-	-	-	-	-	-	-0.07	0.22	0.83
S	-0.02	0.11	0.92	-0.35	1.11	0.3	-0.42	1.38	0.2

[1] Statistics denoted with a "-" could not be calculated as there was either no variation in the data or no data for one of the substrates.

Table 3.2. Average and standard deviations of mineral levels (ppm) measured using inductively coupled plasma mass spectrometry in serum, hair, and antler tissue collected from male and female white-tailed deer (*n* = 28) captured on native rangeland in South Texas, USA during October and November, 2015.

	Serum		Hair		Antler
Mineral	Female (*n* = 14)	Male (*n* = 14)	Female (*n* = 13)	Male (*n* = 14)	Male (*n* = 11)
Calcium	110.81 ± 12.05	112.47 ± 12.90	1346.15 ± 551.25	1335.71 ± 576.80	133563.64 ± 41536.67
Copper	1.15 ± 1.44	1.03 ± 1.05	5.25 ± 2.37	4.03 ± 1.33	7.49 ± 6.20
Iron	11.50 ± 9.10	8.52 ± 6.18	58.14 ± 56.18	54.09 ± 42.14	2361.27 ± 2767.78
Potassium	325.93 ± 174.31	277.57 ± 178.75	2530.08 ± 1630.98	2710.57 ± 1706.15	568.36 ± 502.91
Magnesium	39.61 ± 4.19	39.49 ± 7.26	346.23 ± 173.22	333.57 ± 124.94	5255.45 ± 813.12
Manganese	0.22 ± 0.04	0.20 ± 0.00	2.12 ± 2.09	1.53 ± 1.06	21.21 ± 16.93
Molybdenum	-	-	0.43 ± 0.63	0.30 ± 0.19	1.42 ± 0.30
Sodium	4109.50 ± 363.44	4150.00 ± 179.96	489.23 ± 348.70	470.71 ± 279.99	5186.36 ± 615.83
Phosphorus	194.00 ± 38.83	173.21 ± 34.50	205.38 ± 84.42	185.00 ± 59.45	87154.55 ± 26807.40
Sulfur	1038.57 ± 219.39	1238.71 ± 315.35	23253.85 ± 7080.56	23728.57 ± 5528.17	7653.64 ± 657.20
Zinc	0.40 ± 0.00	0.40 ± 0.00	58.48 ± 23.29	64.88 ± 19.47	49.31 ± 18.84

Table 3.3. Serum mineral concentrations for white-tailed deer captured at the coastal El Sauz site and interior Coloraditas site on native rangelands in South Texas, USA, during October and November, 2015, and corresponding reference values used to determine the proportion of deer that had deficient and above normal serum mineral values (all values are in ppm).

	El Sauz (*n* = 14)			Coloraditas (*n* = 14)		
Mineral	Mean (±SD)	Proportion below deficiency level	Proportion above normal level	Mean (±SD)	Proportion below deficiency level	Proportion above normal level
Calcium	115.74 ± 13.14	0.00	0.07	107.54 ± 10.2	0.00	0.00
Copper	0.2 ± 0.00	1.00	0.00	1.97 ± 1.22	0.21	0.79
Iron	8.34 ± 4.49	0.00	1.00	11.67 ± 9.98	0.00	1.00
Potassium	216.93 ± 49.7	0.00	1.00	386.57 ± 213.61	0.00	1.00
Magnesium	41.96 ± 6.05	0.00	1.00	37.14 ± 4.61	0.00	1.00
Manganese	0.2 ± 0.00	0.00	0.00	0.22 ± 0.04	0.00	0.07
Sodium	4204.29 ± 195.75	0.00	1.00	4055.21 ± 339.23	0.00	0.93
Phosphorus	190.43 ± 34.11	0.00	1.00	176.79 ± 40.83	0.00	1.00
Sulfur	1202.79 ± 305.97	-	-	1074.5 ± 258.21	-	-
Zinc	0.4 ± 0.00	1.00	0.00	0.4 ± 0.00	1.00	0.00

Table 3.3 continued

	Reference Values				
Mineral	Deficient	Marginal	Normal	High	Toxic
Calcium	-	-	85 - 130[2]	-	-
Copper	0.06 - 0.70[1]	0.55 - 0.80[1]	0.80 - 1.50[1]	2.50 - 4.0[1]	4.0 - 11.0[1]
Iron	-	-	0.5 - 3.0[1]	4.0 - 6.0[1]	-
Potassium	-	-	148 - 312[2]	-	-
Magnesium	1 - 18[1]	18 - 20[1]	20 - 30[1]	-	-
Manganese	-	0.0051	0.006-0.03[1]	-	-
Sodium	-	-	3174 - 3450[2]	-	-
Phosphorus	-	-	44 - 90[2]	-	-
Sulfur	-	-	-	-	-
Zinc	0.2-0.4[1]	0.5-0.6[1]	0.7-1.4[1]	1.5 - 5.1[1]	5.2-7.5[1]

[1] Reference values from Puls 1981

[2] Reference values from Puls 1994 (as reported by Creekmore and Glaser 1999)

Table 3.4. Mean and standard deviation for serum mineral levels from lactating and non-lactating female white-tailed deer ≥1.5 yrs. of age captured in 2015 on native rangeland in South Texas, USA, and proportion of individuals that were below published deficiency thresholds.

	Lactating (*n* = 5)		Non-Lactating (*n* = 7)	
Mineral (unit)	Mean ± (SD)	Proportion below deficiency level	Mean ± (SD)	Proportion below deficiency level
Calcium (ppm)	109.88 ± 9.62	0.00	109.13 ± 15	0.00
Copper (ppm)	0.2 ± 0	1.00	1.83 ± 1.71	0.44
Iron (ppm)	8.5 ± 6.75	0.00	14.93 ± 10.98	0.00
Potassium (ppm)	266 ± 81.62	0.00	359.29 ± 230.04	0.00
Magnesium (ppm)	42.74 ± 3.87	0.00	37.97 ± 3.88	0.00
Manganese (ppm)	0.22 ± 0.04	0.00	0.22 ± 0.04	0.00
Sodium (ppm)	4052 ± 406.04	0.00	4162.86 ± 380.34	0.00
Phosphorus (ppm)	176.8 ± 26.32	0.00	193.14 ± 43.02	0.00
Sulfur (ppm)	1034.4 ± 53.42	0.00	1082.43 ± 298.22	0.00
Zinc (ppm)	0.4 ± 0	1.00	0.4 ± 0	1.00

Table 3.5. Parameter estimates produced by von Bertalanffy growth curves for body mass (kg), hind foot length (cm), and antler score (cm; calculated as gross Boone and Crockett score) for female and male white-tailed deer captured at the El Sauz and Coloraditas sites in South Texas, USA, from 2011 – 2019; L_∞ is the asymptotic morphological size estimate, A is the theoretical age when the measured variable would equal 0 which is a meaningless parameter necessary to calculate the growth curve, and K is a growth rate constant.

Site	Sex	Measurement	*n*	L_∞ ± SE	A (years) ± SE	K (years^{-1}) ± SE
El Sauz	Female					
		Body Mass (kg)	744	43.83 ± 0.009	-0.09 ± 0.001	0.92 ± 0.002
		Hind Foot Length (cm)	746	35.21 ± 0.002	-0.32 ± 0.004	2.22 ± 0.010
	Male					
		Body Mass (kg)	462	69.32 ± 0.052	-0.22 ± 0.003	0.44 ± 0.001
		Hind Foot Length (cm)	469	37.38 ± 0.004	-0.58 ± 0.004	1.51 ± 0.006
		Antler Score (cm)	406	334.62 ± 0.654	0.82 ± 0.005	0.38 ± 0.002
Coloraditas	Female					
		Body Mass (kg)	318	48.51 ± 0.030	-0.21 ± 0.005	0.72 ± 0.003
		Hind Foot Length (cm)	318	36.23 ± 0.005	-0.52 ± 0.007	1.71 ± 0.011
	Male					
		Body Mass (kg)	389	86.78 ± 1.225	-0.25 ± 0.002	0.35 ± 0.006
		Hind Foot Length (cm)	390	38.88 ± 0.004	-0.62 ± 0.005	1.36 ± 0.006
		Antler Score (cm)	359	360.82 ± 0.634	0.94 ± 0.006	0.43 ± 0.003

Table 3.6. Mean (± *SD*) of mineral concentrations in soil (2018) and white-tailed deer forage plants samples (2019 and 2020) collected at the El Sauz and Coloraditas sites located in South Texas, USA.

	El Sauz		Coloraditas		Units	
Mineral	Soil	Forage	Soil	Forage	Soil	Forage
Calcium	1117.12 ± 2065.49	1.62 ± 0.89	434.98 ± 88.58	1.80 ± 1.00	ppm	%
Copper	0.27 ± 0.27	7.26 ± 3.22	0.14 ± 0.05	6.85 ± 2.52	ppm	ppm
Iron	8.53 ± 6.23	172.77 ± 129.16	4.18 ± 1.87	175.46 ± 161.28	ppm	ppm
Potassium	130.73 ± 109.12	1.75 ± 0.92	125.67 ± 41.50	1.89 ± 1.02	ppm	%
Magnesium	243.07 ± 297.76	0.36 ± 0.20	81.78 ± 19.31	0.38 ± 0.35	ppm	%
Manganese	7.29 ± 4.20	56.36 ± 38.92	9.23 ± 2.79	52.34 ± 63.23	ppm	ppm
Molybdenum	-	1.22 ± 1.13	-	1.19 ± 1.07	ppm	ppm
Sodium	211.82 ± 444.69	0.14 ± 0.13	2.1 ± 1.00	0.05 ± 0.06	ppm	%
Phosphorus	9.35 ± 6.93	0.17 ± 0.07	9.27 ± 8.34	0.18 ± 0.07	ppm	%
Sulfur	173.49 ± 1000.19	0.29 ± 0.12	3.69 ± 1.10	0.30 ± 0.10	ppm	%
Zinc	0.25 ± 0.28	37.18 ± 27.20	0.33 ± 0.96	37.34 ± 23.87	ppm	ppm

Table 3.7. Statistical test results from Welch's *t*-tests (soil) and paired *t*-tests (forage) comparing mean mineral concentration in soil samples (collected in 2018) and white-tailed deer forage plants samples (collected in 2019 and 2020) from the El Sauz and Coloraditas sites, South Texas, USA.

	Forage		Soil		
Mineral	t_{56}	*P*	*t*	*df*	*P*
Calcium	1.80	0.08	2.16	42.14	0.04
Copper	1.13	0.26	3.10	44.82	0.003
Iron	0.17	0.87	4.41	48.62	<0.001
Potassium	1.28	0.21	0.29	52.60	0.77
Magnesium	0.55	0.59	3.55	42.31	<0.001
Manganese	0.68	0.50	2.57	71.55	0.01
Molybdenum	0.34	0.73	-	-	-
Sodium	4.72	<0.001	3.09	42	0.003
Phosphorus	1.69	0.10	0.04	89.75	0.97
Sulfur	0.48	0.63	1.11	42	0.27
Zinc	0.05	0.96	0.54	56.77	0.59

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