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Original Research

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A B S T R A C T

A growing body of work has revealed that differences in body size of ungulates follow ecoregion and soil boundaries and that these size differences are nutritionally influenced. Currently, it is unclear if these patterns of body size result from differences in quantity or quality of forage produced. We quantified differences in white-tailed deer (*Odocoileus virginianus* Zimm.) body mass and antler size captured at four sites in South Texas, United States. We sampled available forage to determine if long-term differences in average body and antler size could be explained by forage quantity or quality, or some combination of the two. Data collected from 2011 to 2019 indicated female body mass was > 3 kg smaller on the eastern edge of the Coastal Sand Plain ecoregion as compared with those from the western transition zone of the Coastal Sand Plain and Tamaulipan Thornscrub ecoregions. Similarly, male body mass and antler size were > 6 kg and > 20 cm smaller, respectively, in coastal habitats compared with more interior sites. We found that forb biomass, browse and forb diversity, and the nutritional landscape, quantified using digestible energy, crude protein, phosphorus, and neutral detergent fiber, differed between sites. However, differences between sites were inconsistent with predictions that would have supported our hypothesis. Overall, we found no support for the hypothesis that forage quantity drives ecogeographic variation in physical traits of white-tailed deer but were unable to fully refute or support the hypothesis that forage quality, specifically plant diversity, drives ecogeographic variation in physical traits of ungulates.

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Introduction

Geographic variation in body size is a phenomenon long observed in widely distributed taxa. Bergmann's Rule states that organisms residing closer to the poles are larger than their more equatorial counterparts (Bergmann 1847 as in McNab 2010). While Bergmann's Rule is consistent with large-scale gradients in some physiological traits, it is inadequate for describing regional-scale variation in intraspecific size differences (McNab 2010). At regional scales, body size of animals often covaries with soil or vegetation communities (Lehoczki et al. 2011; Cain et al. 2019; Quebedeaux et al. 2019). Furthermore, desert or island populations confound geographic correlations of body size. On the basis of associations of body size with primary productivity, it has been proposed that gradients in body size can largely be explained by a resource rule, where resource availability influences body size via differential allocation of energy from maintenance and reproduction to growth (McNab 2010; Michel et al. 2016).

While the resource rule is a compelling hypothesis, it is difficult to disentangle the drivers of broad- and fine-scale differences in body size of widely distributed taxa. White-tailed deer (*Odocoileus virginianus* Zimm.) are a broadly distributed species of cervid, ranging from Canada to South America. Populations are continuously distributed throughout much of the range, yet up to 38 subspecies have been recognized on the basis of geographic location and minor morphology (Heffelfinger 2011). Genetic studies indicate that the number of subspecies does not reflect the number of unique genetic lineages, and most subspecies are genetically indistinguishable, suggesting many subspecies designations are based more on plasticity of minor morphology rather than inherited genetic differences (Honeycutt 2000; DeYoung et al. 2003). Morphological size
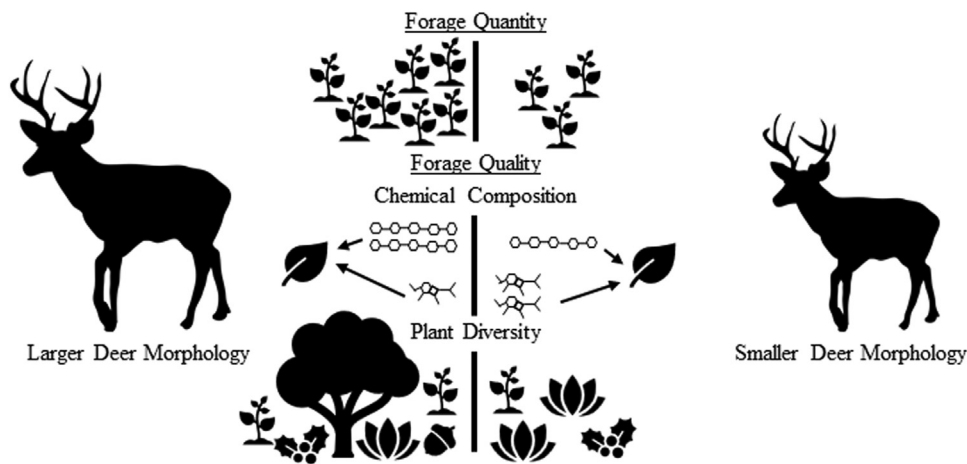
Figure 1. Greater nutrient assimilation is the ultimate driver of variation in ungulate morphology size, yet there are multiple pathways that can mediate difference in nutrient intake. Increased forage abundance (top) or increased forage quality either via difference in nutrient makeup (e.g., increased hemicellulose and decreased lignin content; center) or increased plant diversity, which allows nutrient mixing (bottom).

differences are present both across and within regions, often occurring at fine spatial scales. Recent research suggests that many of the morphological differences that these former subspecies were based on may be nutritionally mediated (Strickland and Demarais 2006; Jones et al. 2010a; Horrell et al. 2015; Cain et al. 2019).

The literature provides many examples of regional differences in body and ornamentation size in ungulates (Gill 1956; Horrell et al. 2015; Quebedeaux et al. 2019). Several studies have correlated regional gradients of ungulate body size with soil properties, which is a proxy for nutrition (Strickland and Demarais 2006; Jones et al. 2010a; 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, as individuals facing nutritional limitation should invest in reproduction over skeletal growth with nutrition beyond what is needed for survival (Monteith et al 2009; Michel et al 2016). Nutrition is likely a driving factor behind regional trends in body size of ungulates, but the drivers of fine-scale variation in nutrition are unclear. A greater level of nutrient intake is the ultimate explanation, yet there are multiple pathways that can lead to this result. For instance, energy intake can be increased by eating more of the same forage or eating forage with a greater energy content, which could be a result of differences in chemical composition of the same forage species or through altering the floristic composition of the diet (Fig. 1).

Regions with more fertile soils produce larger animals because of better nutrition, but it is unclear if fertile soils produce more nutritious plants or simply produce greater forage biomass (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; Dykes et al. 2018; Van Duren and Pegtel 2000). Previous studies revealed that crude protein (Jones et al. 2008) and calcium (Horrell et al. 2015) content of forage increased with increasing soil fertility in some locales, which supports the forage quality hypothesis. In contrast, in a separate study, researchers concluded that quantity of forage was the link between soil productivity and ungulate growth

(Lashley et al. 2015). Plant diversity has also been implicated as a driving factor in regional size differences in ungulates (Strickland and Demarais 2008). The total amount of net primary productivity might be similar between regions, but the amount of useable forage is a function of 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. 2010a; Lashley et al. 2015).

Nutrient acquisition is best thought of as a delicate balancing act. To maximize fitness, living organisms must acquire sufficient nutrients to maintain physiological functioning (Van Soest 1994). Given the limiting nature of many nutrients and minerals in natural settings, range and wildlife managers often discuss nutrition in terms of increasing intake to increase animal performance. For example, increasing energy intake for Cervids generally has positive effects on body and antler growth (Spilinek et al. 2020). Yet an extreme excess of energy intake can also have negative consequences, as seen by the human obesity problems in many modern countries. As such, it is important to remember that while we discuss many nutrients in the context of limitation here, any nutrient or mineral has the potential to be harmful at extreme levels, either low or high (Van Soest 1994). Much of the previous work in Cervid nutrition has focused on the macronutrients and macrominerals, such as digestible energy, crude protein, calcium, and phosphorus (Grasman and Hellgren 1993; Robbins 1993; Jones et al. 2008; Spilinek et al. 2020). The general theme emerging from much of this research is that more is better, within reason. In particular, digestible energy, crude protein, and phosphorus are thought to be limiting nutrients for many terrestrial herbivores (Hewitt 2011). Calcium, while important for lactation and bone and antler development, is generally high in natural forages (Hewitt 2011).

The overall goal of our research was to evaluate the hypotheses that forage quality or quantity are drivers of body size differences in white-tailed deer in the South Texas region. To assess the support for these nonexclusive hypotheses regarding the underlying nutritional drivers of regional size differences in ungulates, we created a priori predictions on the patterns among deer size and forage quantity, nutritive value, and diversity (Table 1). Specifically, we predicted that if forage quantity was driving ecogeographic variation in ungulate morphology, biomass of forbs pre-

Table 1
Predictions for nonexclusive 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, United States; *plus signs* signify larger or greater predicted values, while *negative signs* indicate smaller or lesser values.

	Sites with smaller deer morphometric measurements	Sites with larger deer morphometric measurements
H:1—Forage Quantity		
Aboveground biomass of forbs	−	+
H:2—Forage Quality		
Nutritional content[1]		
Nutrients	−	+
Antiquality compounds	+	−
Forage Diversity		
Shannon-Weiner diversity index	−	+

[1] We quantified multiple nutrients (digestible energy, crude protein, phosphorus, and neutral detergent fiber [NDF]), some of which are usually beneficial (e.g., energy) meaning intake should be maximized, while other elements (e.g., NDF) are antiquality compounds and should be minimized.
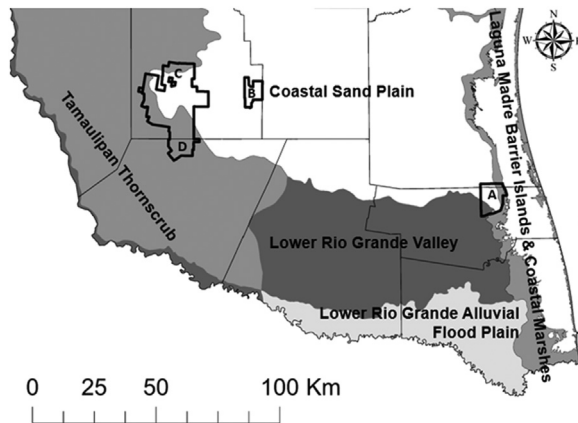

Figure 2. The study was conducted at four spatially unique sites located across the Coastal Sand Plain and Tamaulipan Thornscrub ecoregions of South Texas, United States. Sand content of soils generally decreased from the eastern to western edge of the Coastal Sand Plain ecoregion (**A,** El Sauz, **B,** Buena Vista, **C,** San Antonio Viejo–North, **D,** San Antonio Viejo–South).

Figure 3. Annual precipitation in millimeters per year across our four study sites from 2011 to 2020.

ferred by deer would be greater at sites with larger body mass and antler size. If forage quality was driving ecogeographic variation in white-tailed deer size then 1) digestible energy, crude protein, and phosphorus concentrations would be greater in tested forage plants at sites with larger deer; 2) neutral detergent fiber concentrations would be lower in tested forage plants at sites with larger deer; and 3) forage plant diversity would be greater at sites with larger deer.

Methods

Study area

Our research occurred on four spatially segregated sites located in South Texas, United States (Fig. 2). All sites were owned by the East Foundation, which is an 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 cattle grazing (both continuous year-long and deferred rotational grazing) as part of normal ranching activities and for experimental purposes. Cattle stocking rates ranged from 0 to 37 ha · AU^{-1}. More details pertaining to stocking rates and grazing management can be found in Fulbright et al. (2021). Deer populations on these properties were not hunted or provided with supplemental feed. These unmanaged populations provide us the opportunity to assess hypotheses about drivers of deer body size without complications of differing harvest or management regimes.
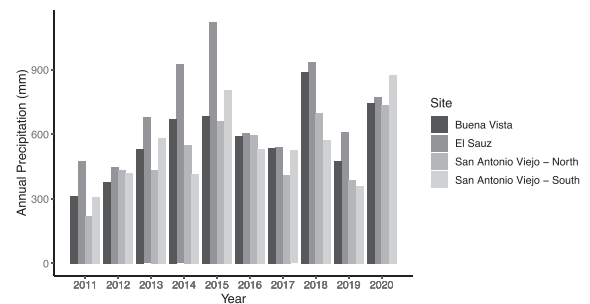
The first of these sites, the El Sauz Ranch (26°34′42.7″N, 97°32′14.52″W), was in Kenedy and Willacy counties. During our study, Willacy County received an average of 71 cm of precipitation annually and the mean yearly high and low temperature was 28.1°C and 18.3°C respectively (2011–2019; PRISM Climate Group 2022; Fig. 3). The eastern border of this 10 984-ha property was the Gulf of Mexico. Soils belonged to the Alfisol and Entisol orders (Hines 2016). Predominate soil series found across our study sites have been described in detail elsewhere (Fulbright et al. 2021). Average sand content of soils on the El Sauz Ranch was 83% (Soil Survey Staff 2020). Vegetation types on the site included deep sand grasslands (52%), salty prairie (9%), deep sand live oak (*Quercus virginiana* Mill.) forest and woodland (8%), deep sand live oak shrubland (6%), active sand dune (5%), sandy mesquite (*Prosopis glandulosa* Torr.) 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 composed of a mixture of 28 other vegetation types (Elliott et al. 2014). Common cacti and woody species found in the area included honey mesquite, live oak, huisache (*Vachellia farnesiana* Wright & Arn.), lime pricklyash (*Zanthoxylum fagara* L.), spiny hackberry (*Celtis ehrenbergiana* Liebm.), brasil (*Condalia hookeri* M.C. Johnst.), and toothache tree (*Zanthoxylum hirsutum* Buckley; Rankins 2021). Graminoids abundant in the area included gulf cordgrass (*Spartina spartinae* Merr. Ex Hitchc.), little bluestem (*Schizachyrium scoparium* Nash), purple threeawn (*Aristida purpurea* Nutt.), and coastal sandbur (*Cenchrus spinifex* Cav.). The number of forb species native to the area was high, and some of the commonly encountered species were Indian blanket (*Gaillardia pulchella* Foug.), American snoutbean (*Rhynchosia americana* M.C. Metz), cardinal feather (*Acalypha radians* Torr.), partridge pea (*Chamaecrista fasciculata* Greene), prostrate fleabane (*Erigeron procumbens* G.L. Nesom), sea oxeye (*Borrichia frutescens* DC.), queen's delight (*Stillingia sylvatica* L.), 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. Mean annual precipitation was 49 cm, and the average annual high and low temperature was 29.5°C and 16.6°C, respectively (2011–2019; PRISM Climate Group 2022). The entirety of this tract of land was located in the Coastal Sand Plain ecoregion (Omernik and Griffith 2014), which was 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* Britton & Rose), Texas hogplum (*Colubrina texensis* A. Gray), lime pricklyash, spiny hackberry, brasil, leatherstem (*Jatropha dioica* Cerv.), tasajillo (*Cylindropuntia leptocaulis* F.M. Knuth), and Texas prickly pear (*Opuntia engelmannii* Salm-Dyck ex Engelm.) were common brush species growing in the western portion of the Coastal Sand Plain (Rankins 2021). Graminoids and forbs common to this site included little bluestem, purple threeawn, coastal sandbur, tanglehead (*Heteropogon contortus* P. Beauv. Ex Roem. & Schult.), hooded windmill grass (*Chloris cucullate* Bisch.), red natal grass (*Melinis repens* Zizka), Indian blanket, partridge pea, Texas senna (*Chamaecrista flexuosa* Greene), woodland sensitive pea (*Chamaecrista calycioides* Greene), widow's tear (*Commelina erecta* L.), hoary milkpea (*Galactia canescens* Benth.), winecup (*Callirhoe involucrate* A. Gray), and woolly croton (*Croton capitatus* Michx.).

The two remaining sites were 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. Although these two sites were located on the same contiguous ranch, they were ~30 km apart, which was approximately the same distance between the Buena Vista and San Antonio Viejo–North sites. The San Antonio Viejo Ranch encompassed 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* Michx.), red lovegrass (*Eragrostis secundiflora* J. Presl), hairy grama (*Bouteloua hirsute* Lag.), cenizo (*Leucophyllum frutescens* I.M. Johnst.), naked Mexican hat (*Ratibida peduncularis* Barnhart), doubtful Texas palafoxia (*Palafoxia texana* DC.), and beebalm (*Monarda* spp.). Mean annual precipitation was 49 cm, and the average annual high and low temperatures were 29.5°C and 16.6°C, respectively, for the northern site (2011–2019; PRISM Climate Group 2022). Mean percent sand of soils at the northern site was 70% (Soil Survey Staff 2020). Soils at this site belonged to the Alfisol order (Hines 2016), while the southern site (26°45′25.20"N, 98°46′11.90"W) had 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 was characterized by thick brush, such as blackbrush (*Vachellia rigidula* Seigler & Ebinger), guayacan (*Guaiacum angustifolium* Engelm.), whitebrush (*Aloysia gratissima* Troncoso), guajillo (*Senegalia berlandieri* Britton & Rose), Texas kidneywood (*Eysenhardtia texana* Scheele), leatherstem, spiny hackberry, brasil, and strawberry cactus (*Echinocereus enneacanthus* Engelm.; Rankins 2021). Buffelgrass (*Pennisetum ciliare* Link) was dominant on the southern site, and forbs were rare but species including widow's tear could be found following episodic rain events. Mean annual precipitation was 50 cm, and the average annual high and low temperature was 30.1°C and 16.7°C at the southern site (2011–2019; PRISM Climate Group 2022).

Deer morphology

From 2011 to 2019, white-tailed deer were captured at the four sites using the helicopter net-gun method (Webb et al. 2008; Jacques et al. 2009). Male and female deer were captured as encountered without regard for age, sex, or physical attributes. By conducting captures each year in October and November before the breeding season, we minimized fluctuations in seasonal body mass change in our dataset and were able to collect measurements from fully formed and mineralized antlers. We collected body mass data to the nearest 0.45 kg using a platform scale. We quantified antler size using the gross Boone and Crockett score (Nesbitt et al. 2009). We assigned each animal an age in 1-yr increments up to a ≥ 6.5 yr of age category, based on tooth wear and replacement (Severinghaus 1949; Foley et al. 2022).

To quantify differences in morphology of white-tailed deer, we fitted three linear mixed-effects models testing for differences in long-term averages of Gross Boone and Crockett score (antler size), female body mass, and male body mass, respectively. We included a random effect term in each of these three models to account for the effect of age. If the overall model indicated there were statistically significant differences between sites at an $\alpha \leq 0.05$ level, we tested for differences in all pairwise comparisons and corrected P values using the Tukey method.

Forage quantity

In our study system there was abundant forage in the form of browse, which is considered adequate for maintenance but may not fully support demands for reproduction and growth (Campbell and Hewitt 2005; Fulbright and Ortega-S. 2013). This abundance of maintenance level nutrition paired with sporadic nutrient pulses in the form of highly nutritious forbs that grow following episodic rain events creates density-independent population dynamics in the absences of supplemental feeding (DeYoung 2011; DeYoung et al. 2019). Therefore, forbs, which represent the high-quality forage available to white-tailed deer in South Texas, are the limiting forage for reproduction in unmanaged systems, while browse only becomes limiting in populations that are supplementally fed (Fulbright and Ortega-S. 2013; DeYoung et al. 2019). Thus, we used aboveground biomass of forbs preferred by deer as determined by Hines et al. (2022) and Fulbright et al. (2021) as a metric of forage quantity. Forb growth predominately occurs during two periods in South Texas, one of which is from September to October (Fulbright et al. 2021). This also coincides with peak graminoid production in the area. Due to logistical constraints imposed by a concurrent study, we chose to collect forb biomass data during the autumn growth peak rather than the spring peak as a representation of accumulated biomass of forbs preferred by deer throughout the growing season (Fulbright et al. 2021). We collected data each autumn (October and November) from 2012 to 2018 on aboveground biomass of forbs preferred by deer using destructive sampling at 50 randomly located 0.25-m^2 quadrats within a 2 500-ha circular area at each of the four sites (Fulbright et al. 2021). The circular boundaries used to delineate our greater sampling areas were approximately centered at original deer capture staging areas and represent the area where deer morphology data were collected (Hines 2016). We dried samples in a forced-air oven to obtain dry matter biomass.

Effects of location, year, and their interaction on forage quantity were assessed with a weighted analysis of variance (Kutner et al. 2004) to accommodate heteroscedasticity (Levene 1960); square root-transformed data were analyzed to improve compliance with normality.

Table 2
Plant species and parts collected for nutritional analysis from four sites located in South Texas, United States, during 2019 and 2020; species chosen were preferred forage plants for white-tailed deer that were typically present at all four sites following Hines (2016).

Scientific name	Common name	Part collected
Acalypha radians Torr.	Cardinal feather	Whole plant
Aphanostephus spp.	Lazy daisy	Whole plant
Callirhoe involucrate A. Gray	Winecup	Whole plant
Celtis ehrenbergiana Liebm.	Spiny hackberry	Growing stem tips
Chamaecrista fasciculata Greene	Partridge pea	Whole plant
Chamaecrista flexuosa Greene	Texas senna	Whole plant
Commelina erecta L.	Widow's tear	Whole plant
Condalia hookeri M.C. Johnst.	Brasil	Growing stem tips
Gaillardia pulchella Foug.	Indian blanket	Whole plant
Opuntia engelmannii Salm-Dyck	Texas prickly pear	Fruit
Prosopis glandulosa Torr.	Mesquite	Bean pods
Ratibida peduncularis Barnhart	Naked Mexican hat	Whole plant
Rhynchosia americana M.C. Metz	American snoutbean	Whole plant
Richardia brasiliensis Gomes	Tropical Mexican clover	Whole plant
Sida lindheimeri Engelm. & A. Gray	Lindheimer's sida	Whole plant
Vachellia farnesiana Wright & Arn.	Huisache	Growing stem tips
Waltheria indica L.	Soldier weed	Leaves
Zanthoxylum fagara L.	Lime pricklyash	Growing stem tips

Forage quality

Nutritive value of forage

We collected 18 commonly encountered plant species (12 forbs, 4 browse, and 2 mast species) preferred by white-tailed deer to compare the nutritive value across sites (Table 2). These were chosen because they occurred on all sites, facilitating an objective comparison of plant nutritive quality among sites. We clipped up to ~50 g wet weight, as available (e.g., some species, such as prickly pear fruit are seasonal in nature or were not present in all plots), of each species within a 50-m radius plot, at 30 randomly located points at each of our 4 sites. These 30 points were a subset of the same points used for biomass sampling, offset by 100 m in a random heading to ensure biomass estimates were unaffected. We collected forage samples during 6 separate 2-wk periods (first 2 wk of April, last wk of May/first wk of June, and last wk of July/first wk of Aug. in 2019 and 2020) to capture phenological and yearly variation in forage nutrition. During each season, we collected samples within a 2-wk period to ensure that phenological differences did not affect site comparisons.

From the 18 plant species that we collected, we dried forage samples in a forced-air oven at 45°C until they reached a constant mass for 48 hr. We 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, we combined equal mass of dried and ground samples. We used an independent laboratory service (Texas Research Institute for Environmental Studies, Huntsville, Texas, USA) to measure phosphorous concentrations using inductively coupled plasma mass spectrometry. Additionally, we contracted the same laboratory service to measure crude protein using the Kjeldahl method (Jurgens 2002). We 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 little temporal variation (Heaney et al. 1963; Givens et al. 1993).

We 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). We 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 our 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, we used 0.25 g of forage sample during sequential fiber analysis, rather than the standard 0.5 g, for spiny hackberry (Teaschner 2006).

We converted gross energy to digestible energy (DE) using a slight modification of the equations developed by Robbins et al. (1987) and Hanley et al. (1992) for white-tailed deer. The first step of this process uses the following equation to determine digestible dry matter (DDM):

$$DDM = [(0.9231e - 0.0451A)(NDF)] + (-16.03 + 1.02\,NDS) \quad (1)$$

The NDF term in this equation is neutral detergent fiber, and neutral detergent soluble (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 $[(ADL - Ash)/NDF] \times 100$, where ADL is acid detergent lignin. We did not include the terms that account for tannins or biogenic silica content of monocots in the earlier equation. Grass consumption by white-tailed deer is generally low (3−11%; Hines et al. 2022); therefore, most authors do not account for the decreased digestibility due to biogenic silica content (Lashley et al. 2015; Gann et al. 2019). Intraspecific variation of condensed tannins in deer forage plants collected across environmental gradients from the southeastern United States has been shown to be insignificant (Jones et al. 2010b). The purpose of our study was to compare nutritional content of the same forage plants across environmental gradients, rather than measuring the absolute digestibility of forage species. Thus, although our digestible energy estimates were potentially inflated for some browse species by not accounting for tannins, the bias is consistent across sites and had no impact on our following analyses. Once we obtained DDM, we calculated DE using the equation:

$$DE = [-0.49 + (0.99 \times DDM)/100] \times GE \quad (2)$$

To test the prediction that nutritional quality might explain observed size differences in deer morphology across sites, we tested for differences between locations in nutritive value of plants. Diet quality is a function of all of the nutrients available in the diet of animals; we selected NDF, crude protein, DE, and phosphorus as the most important nutritional components to characterize. We classified plants into guilds—forbs or browse—for analysis because forbs often are regarded to represent a high-quality forage and browse is more of a maintenance diet (Fulbright and Ortega-S. 2013); we also combined forbs and browse to represent white-tailed deer diets more completely. Both mesquite beans and prickly pear mast were included with browse because they are only available during the summer when deer diets include more browse and mast in South Texas. We conducted univariate analyses that tested for effects of study locations (Buena Vista, El Sauz, San Antonio Viejo–North, and San Antonio Viejo–South), years (2019, 2020), and their interaction on NDF, crude protein, DE, and phosphorus in forbs and browse as separate guilds, as well as forbs and browse combined. Overall diet quality, however, is a multivariate concept that recognizes it is the combination of these nutritional components that represents the diet of a browsing animal. For both univariate and multivariate analyses, our model included location, year, and their interaction as fixed effects; data were analyzed for each sampling period. We used Wilk's λ to test multivariate effects. We used canonical discriminant analysis for data presentation and interpretation; standardized canonical coefficients were used to assess redundancy of variables, and within-location canonical structure was used to interpret canonical variables (Bray and Maxwell 1985; *cf* Rencher 1995; Stevens 2002). We used a normal-score transformation (Mansouri and Chang 1995; Luepsen 2018)

to improve compliance with assumptions of multivariate normality (Mardia 1974; Henze and Zirkler 1990) and homogeneity of variance-covariance matrices (Morrison, 2005); data presentation is on the observed scale.

Richness and Shannon's Index

To determine if forage diversity could account for observed size differences of white-tailed deer between sites, we calculated species richness and the Shannon-Wiener diversity index (Whittaker 1972) from cover of browse species along 28–49, 50-m line transects at each location. Woody plant and cacti presence-absence data were only collected during 2019, since climax vegetation communities of brush often take > 60 yr to develop following disturbance (Fulbright and Ortega-S. 2013). Given the slow growth and long lifespan (i.e., decades) of woody plants in South Texas paired with our interest in comparisons between geographical sites rather than temporal changes, we deemed it unnecessary to repeatedly collect presence-absence data for woody plants and cacti. Throughout much of South Texas, brush grows in mottes or a clumped distribution across the landscape. Thus, using a broad-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 (Canfield 1941).

We also established 50, 0.25-m^2 quadrats in each study location to monitor forb species diversity based on presence-absence data in spring and fall in 2016–2019. Quadrats were located within herbivory exclosures (Fulbright et al. 2021; Himes et al. 2022). Once again, we used the same locations that we used to collect forb biomass and further information on the placement of our points within each site (Fulbright et al. 2021). Because richness (Conover 1999) and Shannon's index (Fritsch and Hsu 1999; Rogers and Hsu 2001) are not normally distributed, we based inferences on permutation-based analysis of variance (Anderson 2017) using the same model used for forage biomass for browse diversity; for forb diversity, analyses were conducted separately for each season because we expected seasonal effects due to the ephemeral nature of forbs. Means and standards errors are presented on the observed scale.

Results

Deer morphology

For our analysis we used a total of 1 751 female body mass measurements, 1 402 male body mass measurements, and 1 277 antler measurements. Mean (±standard deviation) body mass of female deer ≥6.5 years of age at the El Sauz, Buena Vista, San Antonio Viejo–North, and San Antonio Viejo–South sites were 43.32 kg (±4.35), 43.67 kg (±4.06), 47.46 kg (±5.12), and 47.35 kg (±4.66), respectively (Fig. 4). Average body mass for male deer ≥6.5 yr of age were 64.66 kg (±8.00) at the El Sauz, 72.25 kg (±8.26) at the Buena Vista, 77.20 kg (±10.66) at the San Antonio Viejo–North, and 79.10 kg (±8.84) at the San Antonio Viejo–South site (see Fig. 4). Mean gross Boone and Crockett Score for male deer ≥6.5 years of age were 302 cm (±45) at the El Sauz, 303 (±47) at the Buena Vista, 326 (±44) at the San Antonio Viejo–North, and 324 (±57) at the San Antonio Viejo–South site (see Fig. 4).

Female ($F_{3, 1741} = 49.68$, $P < 0.001$) and male body mass ($F_{3, 1392} = 102.23$, $P < 0.001$), as well as gross Boone and Crockett score ($F_{3, 1268} = 26.80$, $P < 0.001$) differed between sites. Mean female body mass after accounting for age was 3.1 kg and 3.2 kg lower at the El Sauz site than the San Antonio Viejo–North ($t_{1741} = 9.39$, $P < 0.001$) and South ($t_{1741} = 8.69$, $P < 0.001$) sites, respectively. Similarly, mean female body mass after accounting for age was 3.0 kg and 3.1 kg lower at the Buena Vista site than

the San Antonio Viejo–North ($t_{1741} = 8.15$, $P < 0.001$) and South ($t_{1741} = 7.61$, $P < 0.001$) sites, respectively. Mean male body mass after accounting for age was 4.2 kg ($t_{1392} = 7.00$, $P < 0.001$), 9.0 kg ($t_{1392} = 15.09$, $P < 0.001$), and 10.3 kg ($t_{1392} = 13.55$, $P < 0.001$) smaller at the El Sauz site compared with the Buena Vista, San Antonio Viejo–North, and South sites, respectively. Mean male body mass after accounting for age was 4.8 kg ($t_{1392} = 7.48$, $P < 0.001$) and 6.1 kg ($t_{1392} = 7.69$, $P < 0.001$) smaller at the Buena Vista site compared with the San Antonio Viejo–North, and South sites, respectively. Mean gross Boone and Crockett score after accounting for age was 27 cm and 28 cm smaller at the El Sauz site than the San Antonio Viejo–North ($t_{1268} = 7.79$, $P < 0.001$) and South ($t_{1268} = 6.26$, $P < 0.001$) sites, respectively. Similarly, mean gross Boone and Crockett score after accounting for age was 20 cm lower at the Buena Vista site compared with the San Antonio Viejo–North ($t_{1268} = 5.38$, $P < 0.001$) and South ($t_{1268} = 4.44$, $P < 0.001$) sites.

Forage quantity

Study location and year of sampling interacted ($F_{18, 1325} = 15.1$, $P < 0.0001$) in their effects on forage standing crop; in addition, location effects were detected ($F_{3, 1325} > 14.96$, $P < 0.0001$) in each year of sampling. For each year, forage standing crop was lower ($F_{1, 1325} > 40.8$, $P < 0.0001$) at San Antonio Viejo–South (larger deer) compared with Buena Vista (smaller deer), El Sauz (smaller deer), and San Antonio Viejo–North (larger deer). Although standing crop did not differ between San Antonio Viejo–South (larger deer) and San Antonio Viejo–North (larger deer) in 2017, in other years, standing crop at San Antonio Viejo–South (larger deer) ranged from 7 to 180 kg ha^{-1} lower than the least productive other study location, and was ~600 kg ha^{-1} lower than Buena Vista (smaller deer) in 2014.

Forage quality

Nutritive value of forage

The nutritional quality of forbs (Tables S1−S3, available online at …) and of browse (Tables S4−S6) generally varied little among locations regardless of sampling period; this pattern applied whether nutritional parameters were analyzed individually or collectively. Year-to-year differences were detected for several dietary parameters when analyzed individually (depending on period), with more detectable yearly differences emerging when parameters were analyzed collectively. In no analysis did location and year interact in their effects on nutritional quality of forbs or of browse. When forbs and browse were combined, however, we detected differences in the nutritional landscape among locations and between years. These patterns were apparent in periods 1 (Table 3, Fig. 5) and 3 (Table 4, Fig. 6) but absent in period 2 (Table 5).

When diet quality parameters of browse + forbs were considered individually in period 1 (early April), location and year acted independently in their effects on NDF, crude protein, DE, and phosphorus (see Table 3). Although we detected location effects on NDF, crude protein, and phosphorus, year effects were detected only for DE, with higher DE in 2020. When dietary parameters were analyzed collectively, both location and year affected diet quality but did so additively. Only the first canonical variable was significant. Crude protein was strongly and positively correlated with the first canonical variable; phosphorus and DE were also positively (but less) correlated with the first canonical variable; NDF, however, was strongly but negatively correlated (see Fig. 5). Furthermore, NDF, crude protein, and DE were approximately equally important along the first canonical variable; phosphorus was less influential in defining this variable. Thus, the essential pattern in the nutritional landscape of browse + forbs during sampling in early April
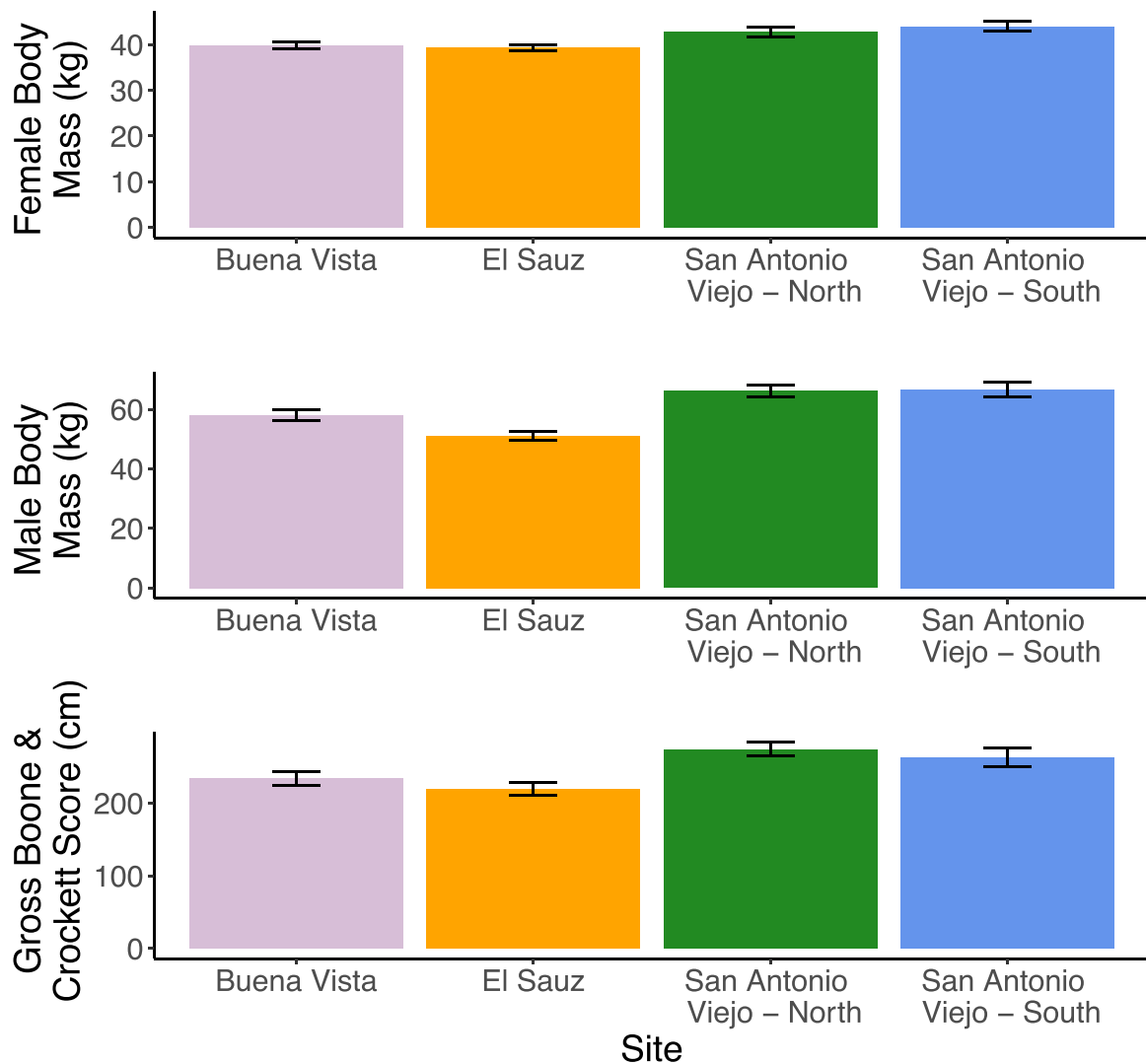
Figure 4. Mean (±95% confidence interval) for female body mass (kg; top), male body mass (kg; middle), and gross Boone and Crockett scores (cm; bottom) for white-tailed deer captured at each of four sites showing that two sites (EL Sauz and Buena Vista) had smaller body and antler sizes in comparison with the other two sites (San Antonio Viejo–North and South).

Table 3

Top: univariate (*F, df, P > F*) and multivariate (Wilk's λ, *df, P > F*) tests of location, year, and location × year effects on diet quality components neutral detergent fiber (NDF), crude protein (CP), digestible energy (DE), and phosphorus (P) for forbs[1] and browse[2] during period 1 (first 2 wk of April). *Bottom*: for the location test, standardized canonical variate coefficients and within-location canonical structure coefficients for canonical variables 1 and 2. Analyses based on normal-score transformed data.

Effect		Univariate tests				Multivariate tests	
		NDF	CP	DE	P	LRT	*P > F*
Location	$F_{3, 74}$	3.84	3.85	1.73	3.15	0.7303	0.0283
	P > F	0.0130	0.0129	0.1687	0.0298	(*df*: 12, 188)	
Yr	$F_{1, 74}$	0.16	0.12	26.70	0.01	0.7286	0.0001
	P > F	0.6885	0.7322	< 0.0001	0.9810	(*df*: 4, 71)	
Location × Yr	$F_{3, 74}$	1.36	0.26	1.18	0.85	0.8745	0.6344
	P > F	0.2627	0.8555	0.3224	0.4717	(*df*: 12, 188)	
Can. Var.	Interpretative coefficients	NDF	CP	DE	P		
1	Standardized coefs	−0.5298	0.4319	0.4844	0.1701		
	Canonical struct	−0.7756	0.8011	0.4251	0.6655		
2	Standardized coefs	0.5081	1.0005	0.8291	−1.0648		
	Canonical struct	0.3028	0.0516	0.5209	−0.4418		

[1] Forb species: cardinal flower, Indian blanket, lazy daisy, partridge pea, naked Mexican hat, Texas senna, Lindheimer's sida, American snoutbean, soldier weed, widow's tear, winecup.

[2] Browse: brasil, spiny hackberry, huisache, lime pricklyash, Texas prickly pear.

Table 4

Top: univariate (*F, df, P > F*) and multivariate (Wilk's λ, *df, P > F*) tests of location, year, and location × year effects on diet quality components neutral detergent fiber (NDF), crude protein (CP), digestible energy (DE), and phosphorus (P) for forbs[1] and browse[2] during period 3 (late July to early August). *Bottom*: for the location test, standardized canonical variate coefficients and within-location canonical structure coefficients for canonical variables 1 and 2. Analyses based on normal-score transformed data.

Effect		NDF	CP	DE	P	LRT	P > F
		Univariate tests				Multivariate tests	
Location	$F_{3, 73}$	0.46	4.44	2.29	4.40	0.7598	0.0715
	P > F	0.7114	0.0063	0.0852	0.0067	(*df*: 12, 185)	
Yr	$F_{1, 73}$	0.02	0.41	15.79	3.75	0.8338	0.0118
	P > F	0.8977	0.5255	0.0002	0.0567	(*df*: 4, 70)	
Location × Yr	$F_{3, 73}$	0.65	0.16	0.72	0.70	0.9167	0.9022
	P > F	0.5878	0.9221	0.5445	0.5569	(*df*: 12, 185)	

Can. Var.	Interpretative coefficients	NDF	CP	DE	P
1	Standardized coefs	−0.0841	0.4846	0.2392	0.6337
	Canonical struct	−0.2592	0.8607	0.4701	0.8386
2	Standardized coefs	0.2769	−0.0541	1.2225	−0.4933
	Canonical struct	−0.2089	0.0581	0.8523	−0.3819

[1] Forb species: cardinal flower, tropical Mexican clover, Indian blanket, lazy daisy, partridge pea, naked Mexican hat, Texas senna, Lindheimer's sida, American snoutbean, soldier weed, widow's tear.

[2] Browse: brasil, spiny hackberry, huisache, lime pricklyash, mesquite.

Table 5

Top: univariate (*F, df, P > F*) and multivariate (Wilk's λ, *df, P > F*) tests of location, year, and location × year effects on diet quality components neutral detergent fiber (NDF), crude protein (CP), digestible energy (DE), and phosphorus (P) for forbs[1] and browse[2] during period 2 (late May to early June). *Bottom*: for the location test, standardized canonical variate coefficients and within-location canonical structure coefficients for canonical variables 1 and 2. Analyses based on normal-score transformed data.

Effect		NDF	CP	DE	P	LRT	P > F
		Univariate tests				Multivariate tests	
Location	$F_{3, 82}$	3.13	0.55	0.51	0.27	0.8578	0.4125
	P > F	0.0299	0.6464	0.6770	0.8438	(*df*: 12, 209)	
Yr	$F_{1, 82}$	0.95	2.53	9.01	0.51	0.8674	0.0226
	P > F	0.3318	0.1153	0.0036	0.4780	(*df*: 4, 79)	
Location × Yr	$F_{3, 82}$	0.18	1.45	2.01	1.69	0.9036	0.7685
	P > F	0.9121	0.2349	0.1192	0.1750	(*df*: 2, 209)	

Can. Var.	Interpretative coefficients	NDF	CP	DE	P
1	Standardized coefs	0.9335	−0.1093	−0.2911	0.3551
	Canonical struct	0.9462	−0.2484	−0.3197	0.0697
2	Standardized coefs	0.4402	1.1308	0.3009	−0.9155
	Canonical struct	0.2311	0.5745	0.2784	−0.2416

[1] Forb species: cardinal flower, tropical Mexican clover, Indian blanket, lazy daisy, partridge pea, naked Mexican hat, Texas senna, Lindheimer's sida, American snoutbean, soldier weed, widow's tear, winecup.

[2] Browse: brasil, spiny hackberry, huisache, lime pricklyash, mesquite.

revealed that San Antonio Viejo–South (larger deer) generally provided a diet higher in crude protein ($F_{1,74} = 10.14$, $P = 0.0021$) and phosphorus ($F_{1,74} = 8.94$, $P = 0.0038$) but lower in NDF ($F_{1,74} = 11.5$, $P = 0.0011$), compared with Buena Vista (smaller deer), El Sauz (smaller deer), and San Antonio Viejo–North (larger deer); however, we did not detect differences ($F_{1,74} = 1.77$, $P = 0.1880$) in diet quality among Buena Vista (smaller deer), El Sauz (smaller deer), and San Antonio Viejo–North (larger deer).

In period 3 (late July to early August), location and year acted independently in their effects on nutritional parameters when analyzed individually (see Table 4). Location effects were detected for crude protein, phosphorus, and to a lesser extent, DE; NDF did not vary among locations. As observed in period 1, these location effects were largely manifested in a difference between San Antonio Viejo–South (larger deer) and the other sites, but no differences among the other sites. In particular, phosphorus, crude protein, and to a lesser extent, DE were higher at San Antonio Viejo–South (larger deer) than at the other sites, with no differences among the other sites. Location effects were also detected ($P = 0.07$) when NDF, crude protein, DE, and phosphorus were analyzed collectively. Crude protein and phosphorus were strongly and positively correlated with the first canonical variable, whereas DE was positively but more weakly correlated with the first canonical variable; NDF was negatively correlated with the first canonical variable and its correlation was weaker than observed for crude protein and phosphorus (see Fig. 6). Phosphorus and, to a lesser extent, crude protein were the most influential variables separating location means along the first canonical axis. Overall, patterns detected in the nutritional landscape of browse + forbs in late July to early August (period 3, see Fig. 6) were similar to patterns detected in early April (period 1, see Fig. 5).

Richness and Shannon's Index

Location and year of sampling interacted in their effects on forb richness in spring ($F_{9, 784} = 5.63$, $P < 0.001$) and in fall ($F_{9, 784} = 9.43$, $P < 0.001$) and on Shannon's index in spring ($F_{9, 607} = 4.85$, $P < 0.001$) and in fall ($F_{9, 494} = 4.25$, $P < 0.001$; Fig. 7). Generally, patterns in richness and diversity were similar across locations for a given season and year of sampling—these two metrics reflected each other. Richness ranged from 0 to 10 species at the quadrat level and averaged from 0.14 ± 0.07 to 4.6 ± 0.4 species per quad across the eight sampling periods analyzed; depending on period analyzed, a difference of one species was significant. Although location differences were detected in every season-
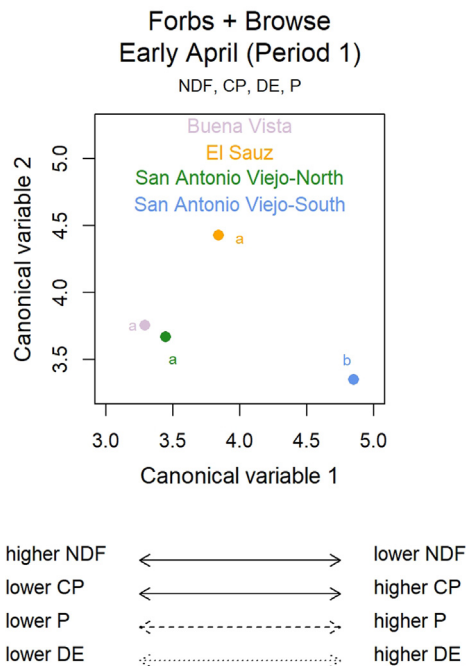
Forbs + Browse
Early April (Period 1)
NDF, CP, DE, P

Figure 5. Canonical discriminant analysis display of location means for Buena Vista (smaller deer), El Sauz (smaller deer), San Antonio Viejo–North (larger deer), and San Antonio Viejo–South (larger deer) with respect of neutral detergent fiber (NDF), crude protein (CP), digestible energy (DE), and phosphorus (P) in early April (Period 1). Means followed by the same lowercase letter are not significantly different ($P > 0.05$). *Arrows* illustrate correlations between diet quality variables and the first canonical variable; strength of correlation is highest for *solid arrows,* intermediate for *dashed arrows,* and lowest for *dotted arrows.*

Forbs + Browse
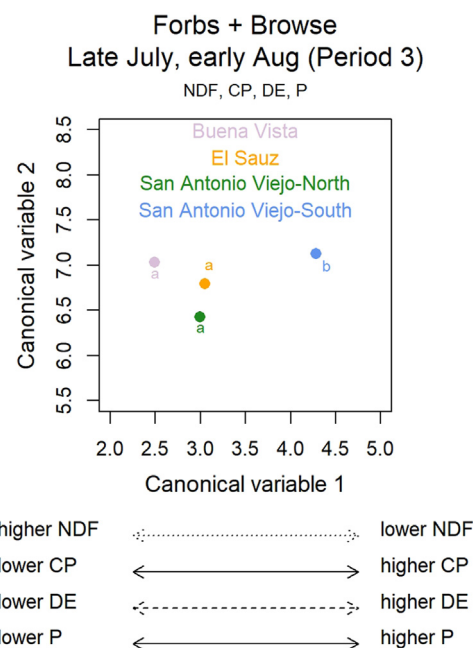## Late July, early Aug (Period 3)
NDF, CP, DE, P

Figure 6. Canonical discriminant analysis display of location means for Buena Vista (smaller deer), El Sauz (smaller deer), San Antonio Viejo–North (larger deer), and San Antonio Viejo–South (larger deer) with respect to neutral detergent fiber (NDF), crude protein (CP), digestible energy (DE), and phosphorus (P) in late July to early August (Period 2). Means followed by the same lowercase letter are not significantly different ($P > 0.05$). *Arrows* illustrate correlations between diet quality variables and the first canonical variable; strength of correlation is highest for *solid arrows,* intermediate for *dashed arrows,* and lowest for *dotted arrows.*

year combination, the only generalizations apparent in these responses are that San Antonio Viejo–South (larger deer) 1) had the lowest species richness and 2) usually the lowest diversity. However, the location with highest richness or diversity varied among season-year combinations.

Browse species richness ($F_{3, 166} = 46$, $P < 0.0001$; Fig. 8, bottom) and Shannon's index ($F_{3, 166} = 27.1$, $P < 0.0001$; see Fig. 8, top) differed among study locations. We observed highest richness (9.8 ± 0.58 species per transect) at San Antonio Viejo–South (larger deer) and lowest (2.5 ± 0.30 species per transect) at El Sauz (smaller deer). Similar trends were observed for Shannon's index. Additionally, San Antonio Viejo–South (larger deer) had higher richness ($F_{3, 166} = 114.8$, $P < 0.0001$) and Shannon's index ($F_{3, 166} = 48.2$, $P < 0.0001$) compared with Buena Vista (smaller deer), El Sauz (smaller deer), and San Antonio Viejo–North (larger deer).

Discussion

Gradients in soil and vegetation communities explain many patterns of regional body size and antler growth in Cervids (Gill 1956; Strickland and Demarais 2006; Jones et al. 2010a; Lehoczki et al. 2011; Horrell et al. 2015; Cain et al. 2019; Quebedeaux et al. 2019). We found that female body mass was smaller on the eastern edge of the Coastal Sand Plain ecoregion as compared with those from the transition zone of the Coastal Sand Plain and Tamaulipan Thornscrub ecoregions. Similarly, male body mass and antler size were smaller in coastal habitats compared with more interior sites. Furthermore, we detected differences in forage quantity and forage quality (both in the nutritive value and diversity of forage) among sites. However, the nutritional data were inconsistent with respect to clear drivers of body size.

There is ample circumstantial evidence that nutrition is the likely ultimate driver of body size in our study system. The two sites with smaller body mass and antler sizes were situated on the Coastal Sand Plain ecoregion (Omernik and Griffith 2014). The two sites that 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 (Fulbright et al. 1990; Peacock and Smith 2020). 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 (Olorunfemi et al. 2016). In times of plentiful rain, the Coastal Sand Plain ecoregion is highly productive, but due to the low water retention capabilities of the soil, many forbs that grow in the area are ephemeral in nature (Fulbright and Ortega-S. 2013).

Although our results confirmed biologically meaningful differences in deer body size among study sites, the nutritional analyses revealed complex patterns, some of which ran counter to our a priori expectations. Previous studies have demonstrated the nutritional importance of forbs as a driver of reproduction and body condition in the semiarid region of South Texas (Gann et al. 2019). More broadly, yearly and seasonal differences in forb production can be responsible for reproduction and seasonal differences in body condition of ungulates (Simard et al. 2014). This finding has in some respects devalued the importance of browse as primarily a maintenance food for adults but inadequate to support the nutritional demands of lactation and antler growth.

We expected annual fluctuations in forb production and annual variation in forb growth due to variable amount and timing of precipitation. Ungulate growth and development are often influenced by forage quantity through conspecific competition for forage (i.e., density-dependent mechanisms; Borowik and Jędrzejewska 2018;
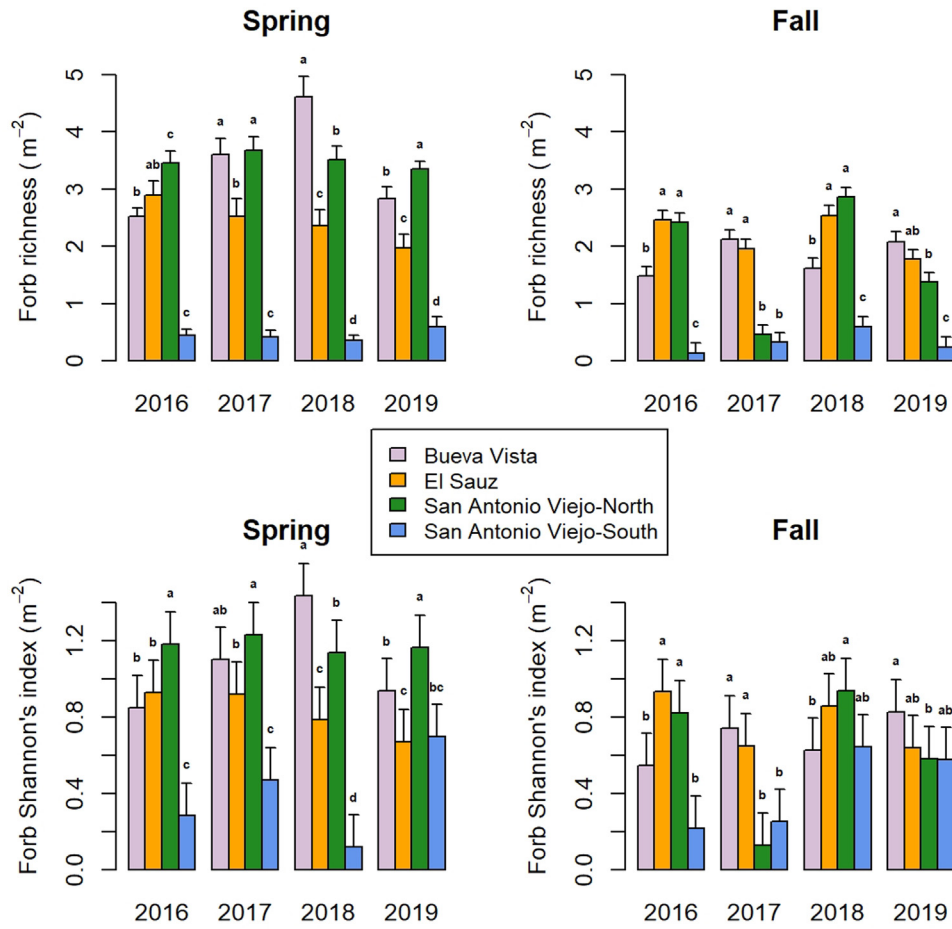
Figure 7. Mean ± (sem) forb species richness (bottom) and Shannon's index (top) for spring (left) and fall (right) seasons as affected by year and study location. Means for a given metric followed by the same lowercase letter are not significantly different ($P > 0.05$, protected least significant difference test).
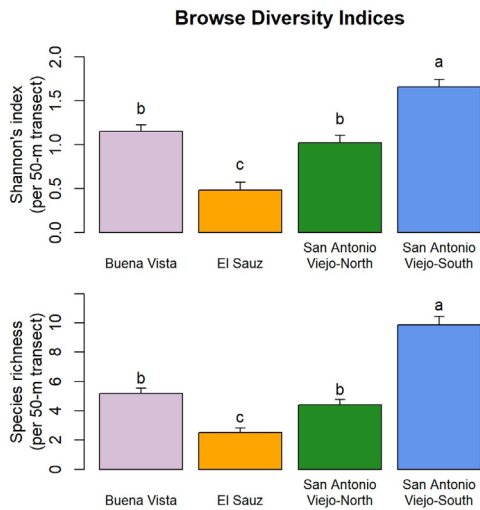

Figure 8. Mean ± (sem) browse species richness (bottom) and Shannon's index (top) as affected by study location. Means for a given metric followed by the same lowercase letter are not significantly different ($P > 0.05$, protected LSD test).

Zubillaga et al. 2018; Kavčić et al. 2019). However, due to the highly variable nature of rainfall (Crider et al. 2015), unmanaged populations of white-tailed deer in the South Texas region rarely reach densities high enough to induce intraspecific competition for forage. This is because resource pulses that enable reproduction are more influenced by precipitation than population density (DeYoung 2011; DeYoung et al. 2019). The site with the consistently lowest forb production, however, was one of the sites with the largest body mass and antlers sizes. Therefore, our hypothesis that sites with more forb biomass should produce larger deer was not supported.

The hypothesis for a resource rule that explains differences in body size posits that nutritional cues should induce animals to shift from investing in skeletal or somatic growth to maximize reproduction (McNab 2010). However, the time scale over which this nutritional cue operates is uncertain. Our results suggest that the importance of variable forb pulses in semiarid regions may influence deer nutrition at finer (within-year) temporal scales but may not provide the signal that cues ungulates to reduce allocation of resources to skeletal growth in favor of maximizing reproduction.

Unlike previous studies (Jones et al. 2008; Horrell et al. 2015), we found no evidence for a site effect on the nutritional values of common plants; the plant species in common to all sites were of similar nutritional value. Our data suggest that the nutritional landscape was higher quality at one of the sites with larger deer yet was of lower quality and consistent at the other three sites (two with smaller deer and one with larger deer). The San Antonio Viejo–South site (larger deer) had higher forage quality (increased DE, crude protein, phosphorus, and lower NDF), partially supporting our hypothesis that forage quality drives ecogeographic variation in ungulate morphology. However, there was no difference between the San Antonio Viejo–North (the second site with larger

deer sizes) and the two sites with smaller deer sizes, which is inconsistent with predictions for site effects. Although we did detect a difference in the nutritive value of forage at one of the sites with larger deer (San Antonio Viejo−South), this difference was a result of species composition. This site was characterized by predominately woody plants, with little forb availability in comparison with the three other sites. The differences in DE, crude protein, phosphorus, and NDF that we detected are indicative of a difference between browse and forbs, rather than differences in the same forage between sites. Furthermore, these differences between the nutritional quality of forbs and browse are likely an artifact of our sampling scheme−the whole plant was sampled for forbs and only growing stem tips and leaves were sampled for browse. Therefore, the true site differences that we detected are browse richness and diversity.

By these measures of nutritive value, our data do not support the hypothesis that site differences in forage quality drive localized differences in ungulate morphology. Nonetheless, we acknowledge that by definition, forage quality is best measured by animal performance and is therefore difficult to assess (Van Soest 1994). As a proxy for nutritional quality, we measured several nutrients and elements important to physiological functioning of ruminants. These represent point estimates from a defined time period. However, diet selection is a dynamic process involving animal choices on a daily to weekly basis (DeYoung et al. 2019), as animals of differing physiological states select a diet that best meets their needs (Provenza et al. 2003). Clearly, there are many other nutrients and chemical compounds that influence deer nutrition that we did not measure.

The hypothesis that plant diversity is important for a concentrate selector such as white-tailed deer is intuitively appealing. We found that the site with the higher-quality nutritional landscape (San Antonio Viejo–South) generally had greater browse diversity. We also found that one of the sites with smaller deer sizes had the lowest browse diversity. However, we detected no difference in browse diversity between the other two sites (one with larger deer and one with smaller deer). In contrast, forb richness and diversity were in direct opposition to our prediction, as one of the sites with larger deer consistently had the lowest forb richness and diversity (San Antonio Viejo–South; see Fig. 7). These results are counter to the conventional wisdom about the importance of forbs to deer nutrition. The lack of clear support for the importance of forbs to deer body sizes implies that the year-round diet quality provided by browse may be more important as a nutritional cue for skeletal growth. Alternatively, deer may be able to meet their nutritional requirements if either browse or forb diversity is available or may be able to meet some of their requirements from food items we did not measure, such as grasses.

The hypothesis that greater forage plant diversity provides greater nutrition is not explicitly tested but is often an inherent assumption in studies examining the benefits of migratory strategy in rangeland ungulates (Schuyler et al. 2021). Plant diversity partially explained regional size differences of deer in forested landscapes of Mississippi, in absence of agronomic crops (Strickland and Demarais 2008). There has been much research published postulating that migratory ungulates throughout the world benefit by surfing the "green wave" or having prolonged exposure to phenologically young and more nutritious forage (Hebblewhite and Merrill 2009; Aikens et al. 2020a; Aikens et al. 2020b). For nonmigratory ungulates, including those in our study system, being exposed to a greater diversity of forage plants increases the odds that at any one time there will be a plant species that is in the emergent or growth stage. Thus, higher forage plant diversity allows nonmigratory ungulates to surf the "green wave" by letting the waves come to them, rather than tracking the wave. Furthermore, mixing the types of forages that they consume allows herbivores to maxi-

mize 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). The idea that regional body mass and antler size of deer are driven by floristic composition is intriguing, but further research is needed to fully evaluate this hypothesis.

We tested hypotheses for common drivers of body size, but the underlying nutritional mechanism driving deer size differences may vary between sites. Indeed, even among studies that have found support for the forage quality hypothesis, there is little agreement as to which specific nutrient(s) are limiting. For example, previous studies conducted in mesic environments of the southeastern United States, where annual rainfall is more consistent, found that crude protein and calcium might explain regional size differences in body mass and antler size of white-tailed deer (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, it was found that minerals, including calcium, copper, zinc, phosphorus, and manganese, could be regionally limiting for moose (*Alces alces* L.) populations in northwest Wyoming (Becker et al. 2010). A recent study found some evidence that minerals may be limiting at one of our study sites with small deer sizes (Rankins et al. 2023). Clearly there is a need for more research to determine which nutrient(s) are limiting. From a broader ecological viewpoint, our data are not conclusive as to nutritional drivers of body size in our study system but do lend some support to forage diversity hypotheses. Thus, our results are consistent with the idea that a resource rule can explain geographical variation in body size.

Ecologists have postulated overarching rules or laws that explain geographic variation in morphology for centuries (McNab 2010). While some of these rules have stood the test of time and are broadly applicable (e.g., Bergmann's Rule; Bergmann 1847 as in McNab 2010), they often fail to account for geographic variation in morphology at regional scales (McNab 2010). Yet such geographic variation is present and well documented in many taxa (Lehoczki et al. 2011; Cain et al. 2019; Quebedeaux et al. 2019). Historically, many regional, or subregional, differences in morphology have been attributed to genetic differences and have been the basis for subspecies designations (Heffelfinger 2011). More current research often refutes the notion that such geographical differences in morphology arise from genetics (Honeycutt, 2000; DeYoung et al. 2003). Our data contribute to a growing body of work suggesting that these differences are largely due to differences in geology, climate, and vegetation communities, which give rise to differences in nutrition (resources; Lehoczki et al. 2011; Cain et al. 2019; Quebedeaux et al. 2019).

Implications

Overall, our data suggest that substantial differences in morphology of mammals at fine geographic scales may be due to differences in geology, climate, and vegetation communities, which give rise to differences in nutrition. This further supports the idea of a resource rule, or the idea that nutritional resources are the primary driver of size differences in organisms inhabiting similar latitudes (McNab 2010). The proximate components of the nutritional environment that cue differential investment in skeletal growth appear more elusive and nuanced. We found no support for our hypothesis that differences in forage quantity among sites drive ecogeographic variation in physical traits of deer in our study system. However, our data provide uneven support for the hypothesis that forage quality, measured as nutritive value and diversity of forage, is the driver of fine-scale geographic differences in ungu-

late morphology. Understanding the nutrient limitations imposed on mammalian growth inherent to some regions will help managers set reasonable goals and expectations. Additionally, understanding the large impact of nutrition on the growth potential of ungulates will allow managers to focus their attention on an attainable goal of improving the nutrition available to animals.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2023.01.005.

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