ARTICLE

Fine-scale phenotypic variation of a large herbivore in a pulsed environment

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Abstract

The resource rule hypothesis predicts that geographic differences in body size among populations of organisms are due to the amount, availability, and quality of food resources. For instance, the body size of large herbivores is often correlated with soil characteristics because better soils produce better forage. In semiarid environments, rainfall variation is an important driver of forage availability, especially highly nutritious annual forbs. Thus, in such pulsed-resource environments, it is unclear whether the body size of large herbivores is influenced by fixed resources correlated with soil characteristics, irregular resource pulses correlated with rainfall, or both. Furthermore, it is not clear whether phenotypic expression is a function of forage quality or quantity. During the early autumns of 2011–2018, we captured 4554 white-tailed deer (*Odocoileus virginianus*) on seven rangeland sites in the semiarid climate of South Texas, USA. The sites range from coastal to 140 km inland and represent gradients in both soil texture and annual rainfall. We recorded age- and sex-specific indices of skeletal size, antler size, and body mass. Site-specific soil characteristics explained most of the variation in skeletal size; percent sand was inversely related to skeletal size. For environmentally sensitive phenotypes (antler size and body mass), both soil characteristics and rainfall were influencers; increases in rainfall reduced the negative effect of sand. Percent sand and rainfall were positively correlated with annual biomass of preferred forbs, yet all phenotypic traits declined with increases in forb quantity. Increases in percent shrub cover increased all phenotype sizes. Our data suggest that the phenotypic expression of large herbivores in semiarid environments is driven by forage quality via edaphic characteristics rather than forage quantity via rainfall. Specifically, less sand in the soil allows for the development of shrub communities, which in turn provide a consistent source of forage in a variable, pulsed-rainfall environment. Although forbs are of higher quality, they are highly ephemeral. The availability of a consistent source of forage may enable white-tailed deer to extend time invested in body

growth, which results in greater phenotype size. Our findings align with the resource rule hypothesis that identifies resource availability as a fundamental element explaining geographical variation in phenotypic expression.

KEYWORDS

phenotype variation, pulsed envrionments, resource rule hypothesis, white-tailed deer

INTRODUCTION

Phenotypes are observable, quantitative traits of an individual. Phenotypes are genetically determined, but the expression of traits is influenced by the environment (Post et al., 1997; Post & Stenseth, 1999; Toigo et al., 2006). Environmental gradients in phenotypes have led ecologists to propose "rules" explaining differences in phenotypic expression among animal populations. For instance, variation in body size has been attributed to latitude (Bergmann's rule; Bergmann, 1847), desert climates (Yom-Tov & Geffen, 2006), islands (the Island rule; Foster, 1964), and evolutionary time (Cope's rule; Cope, 1887). The different "rules" for variation in body size have exceptions, resulting in lack of clarity on drivers of animal phenotypes. McNab (2010) argued that the different "rules" all have one fundamental element in common: resource availability. In McNab's hypothesized "resource rule," animals face a trade-off between investing in skeletal growth versus reproduction. When more resources are available, more energy can be invested toward growth, resulting in larger phenotype sizes (Mattioli et al., 2021; Monteith et al., 2014). If resources are limited, animals cease growth earlier to invest in reproduction (Simard et al., 2008). The differences in resource availability may result in long-lasting, intergenerational effects on phenotypic expression (Michel et al., 2016; Monteith et al., 2009). Occasionally, phenotypic differences within the same species are so extreme that populations are classified (incorrectly) as subspecies (Patten, 2015; Patten & Remsen, 2017).

Permanent environmental conditions that influence phenotypes in large herbivores include soil characteristics. Soil fertility, a relatively constant characteristic of an environment, positively influenced body and antler size of white-tailed deer (*Odocoileus virginianus*), resulting in a gradient in phenotype size (Jones et al., 2010; Strickland & Demarais, 2000). Because soil fertility influences forage characteristics, namely nutrition (Gaillard et al., 1996; Hefley et al., 2013; Herfindal et al., 2006; Pettorelli et al., 2001; Simard et al., 2008), there is a link between edaphic-driven forage and phenotypic expression (Bowyer et al., 2002; Mattioli et al., 2021;

Ramanzin & Sturaro, 2014). However, forage needs moisture to grow and moisture is typically derived from the environment. In temperate environments, precipitation is relatively consistent compared with semiarid environments. In semiarid environments, rainfall is highly variable and influences both forage quality and quantity, resulting in irregular resource pulses (Chesson et al., 2004). Large herbivores in pulsed environments respond strongly to rainfall in terms of reproduction and body condition (Heffelfinger et al., 2018; Marshal et al., 2005; Ogutu et al., 2014) because of the release from limited nutrition (DeYoung et al., 2019). However, it is not clear whether phenotypic size limitations associated with poor soils or variable rainfall are due to limited forage quantity or quality (Lashley et al., 2015).

The expression of phenotypic traits in animals can be an indicator of genetics, adaptation, and fitness, which allows insights into selection and the evolution of life histories (Pigeon et al., 2017; Pigliucci, 2003). Long-term studies in variable habitats, such as semiarid environments, are lacking (Festa-Bianchet et al., 2017, but see Rankins, DeYoung, Wester, et al., 2023). The strong interplay between rainfall and phenotypic characteristics of large herbivores in semiarid environments poses several important, unanswered questions: What role do soil characteristics have in the phenotypic expression of large herbivores in a pulsed environment that can change from a desert to a lush landscape, depending on rainfall? Do infertile soils reduce the positive effect of the increased forage quality and quantity that is produced by rainfall? Are phenotypic sizes of large herbivores responding to the increased forage quantity generated by rainfall or is the response from increased forage quality?

We used 7 years of white-tailed deer capture data from semiarid South Texas, a variable, pulsed environment (DeYoung et al., 2019), to quantify the relationship between soil characteristics and rainfall on phenotypic expression. Our dataset included deer captured on a gradient of soil characteristics and annual rainfall, which made for an ideal opportunity to test hypotheses related to phenotypic expression. Because soil characteristics are a more permanent environmental condition than the temporally variable rainfall, we hypothesized that

phenotype size would decline as soil became less fertile (i.e., increase in percent sand) regardless of rainfall. Because white-tailed deer are concentrate-selectors (Spalinger, 2000), we also hypothesized phenotypic expression would be correlated with proxies of forage quality rather than forage quantity.

METHODS

Study sites

Our research took place on four rangeland sites in South Texas, USA (Figures 1 and 2) that were operated by the
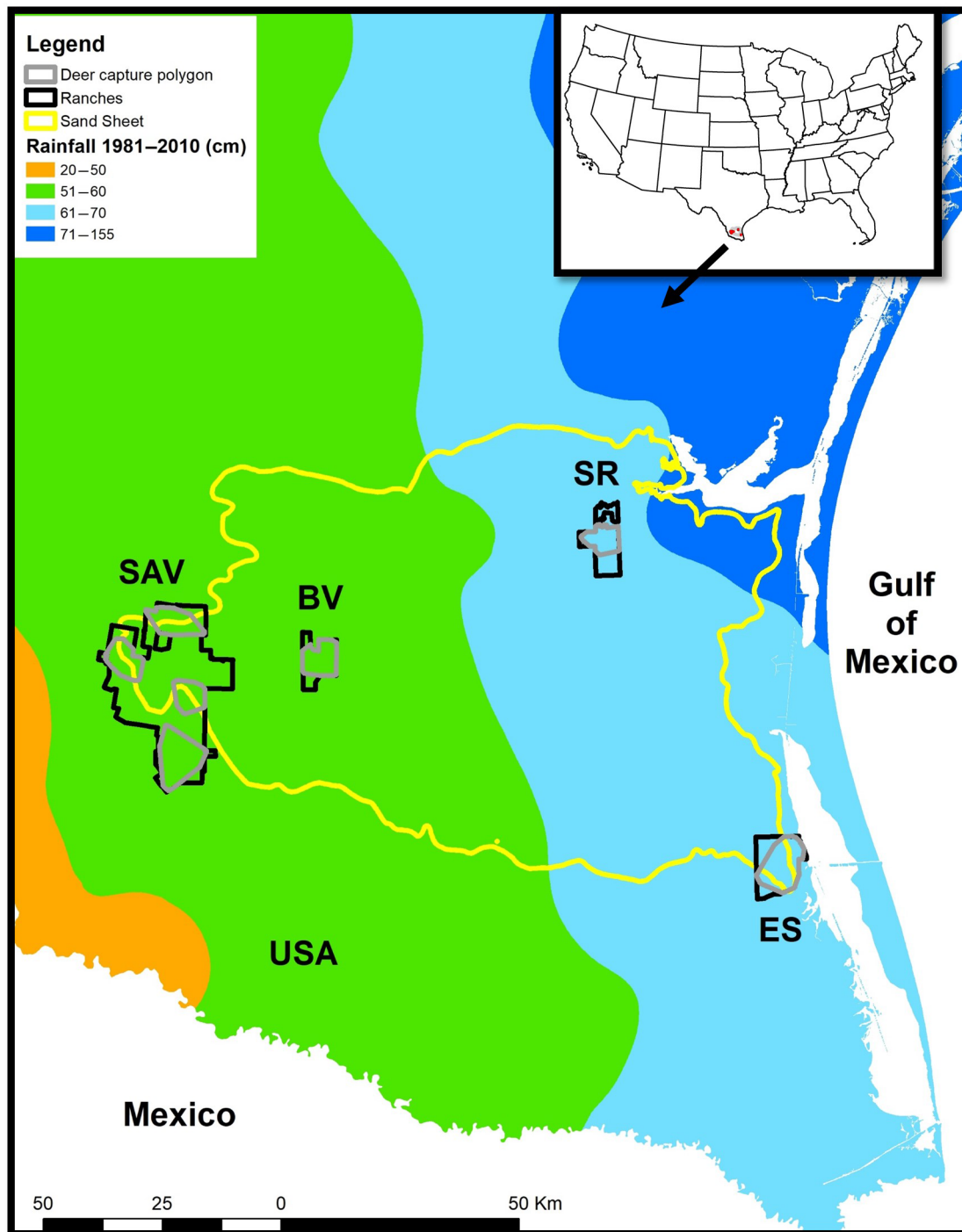
FIGURE 1 White-tailed deer capture sites ($n = 7$) within four East Foundation ranches in South Texas, USA, during 2011–2018. Capture site polygons were created by generating a minimum convex polygon that were clipped by ranch boundaries. Sand sheet is a region characterized by migrating sand dunes. BV, Buena Vista; ES, El Sauz; SAV, San Antonio Viejo; SR, Santa Rosa.
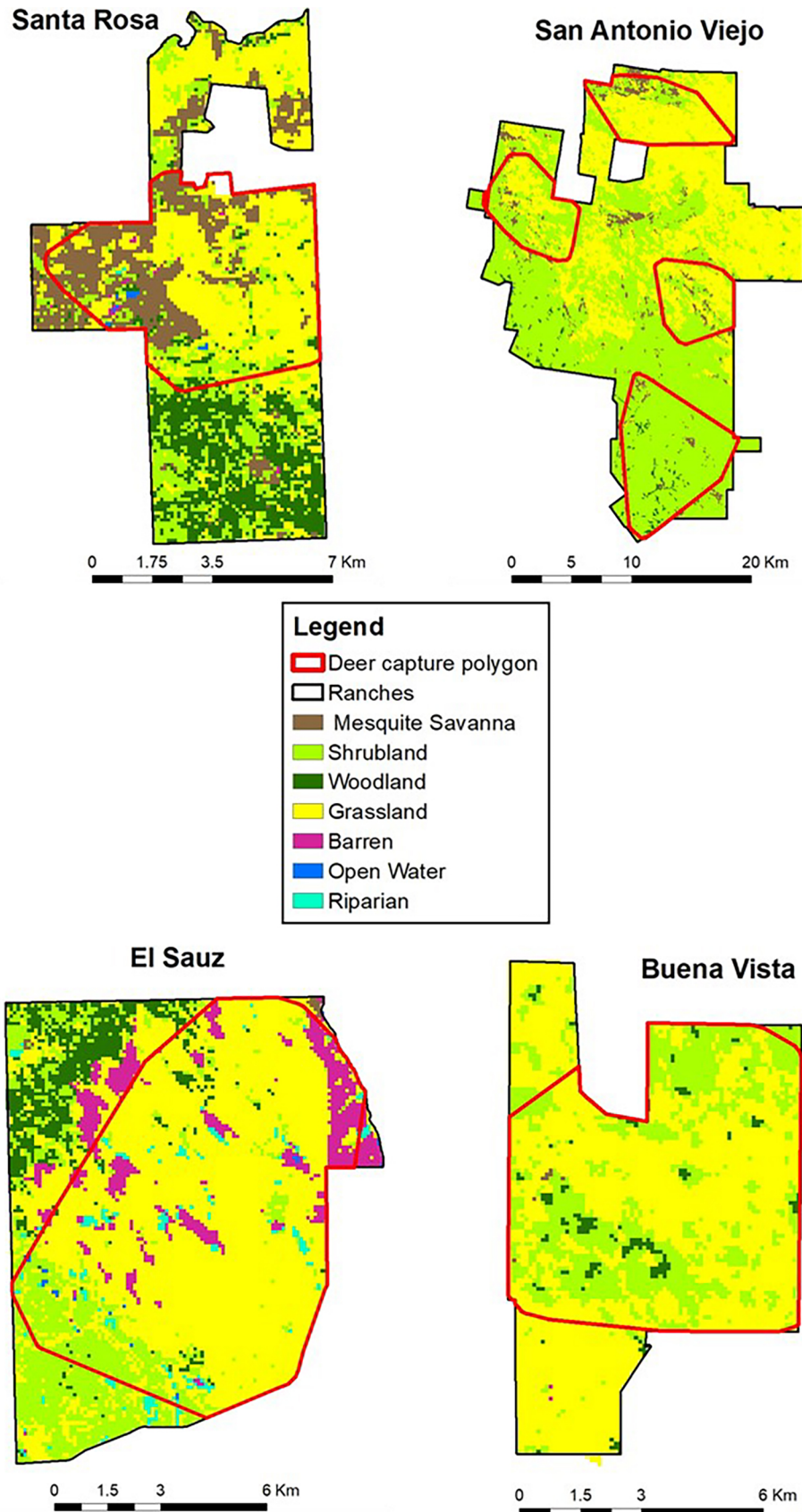
FIGURE 2 Habitat characteristics of the seven capture sites within four East Foundation ranches in South Texas, USA, during 2011–2018. Capture site polygons were created by generating a minimum convex polygon that were clipped by ranch boundaries. Ecoregion shapefile source: Texas Parks and Wildlife Department.
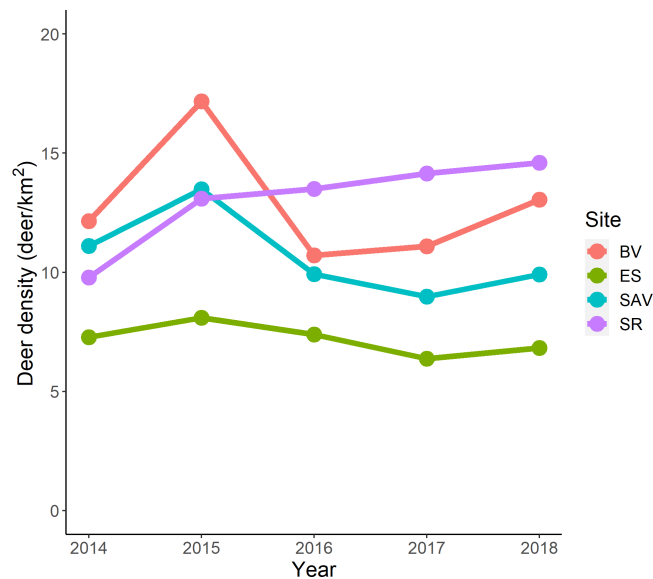
FIGURE 3 Estimated deer densities for the four East Foundation ranches in South Texas, USA, acquired via helicopter-based distance sampling methods during winter 2014–2018. BV, Buena Vista; ES, El Sauz; SAV, San Antonio Viejo; SR, Santa Rosa.

East Foundation, an Agricultural Research Organization that promotes the advancement of land stewardship through ranching, science, and education (www.eastfoundation.net). The sites were operated as working ranches grazed by cattle as part of normal ranching activities; grazing included continuous year-long and deferred rotational grazing. Cattle stocking rates ranged from 0 to 37 ha/animal units $(AU)^{-1}$. 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 nutrition (Jacobson et al., 2011). These unmanaged populations provide us the opportunity to assess hypotheses about phenotypic size of white-tailed deer without the complications of differing harvest or management regimes.

The four sites exist on a gradient from the coast to about 140 km inland, which results in varying soil types and vegetation and communities. The region also contains the "South Texas Sand Sheet," where eolian sand deposits from the Gulf of Mexico form a veneer of sand <3 m deep, with the presence of active sand dunes (Forman et al., 2009). The El Sauz Ranch (10,984 ha) is adjacent to the Gulf of Mexico (26°34′42.7″ N, 97°32′14.52″ W) and moving inland is the Santa Rosa Ranch (7544 ha, 27°10′58.8″ N, 97°51′39.6″ W, 46 km from the Gulf of Mexico), the Buena Vista Ranch (6113 ha, 26°57′30.36″ N, 98°25′5.16″ W, 108 km from the Gulf of Mexico), and the San Antonio Viejo Ranch (60,034 ha, 26°53′11.45″ N, 98°47′43.08″ W, 140 km from the Gulf of Mexico). The San Antonio Viejo Ranch was

broken up into four distinct capture sites: San Antonio Viejo-North, San Antonio Viejo-South, San Antonio Viejo-East, and San Antonio Viejo-West (Figures 1 and 2). All ranches were entirely within the Western Gulf Coastal Plain except for San Antonio Viejo, which is partially within the Southern Texas Plains (Omernik & Griffith, 2014). In addition to variation in vegetation and soil communities, rainfall in this region is highly variable and decreases from coastal (CV = 20%) to inland (CV = 37%, Parylak, 2010). Additional information regarding site-specific plant and soil communities can be found in Fulbright et al. (2021). Deer densities were estimated by helicopter-based distance sampling (Peterson et al., 2020) during the winter of 2014–2018; deer densities were similar with the exception of El Sauz, which had the lowest density (Figure 3). Other herbivores present included native collared peccary (*Pecari tajacu*), free-ranging exotic nilgai antelope (*Boselaphus tragocamelus*), and feral pigs (*Sus scrofa*).

Capture

During October and November 2011–2018, we captured deer as encountered via helicopter net-gunning (Webb et al., 2008). Captured deer were hobbled and blindfolded, and a GPS waypoint was recorded at the capture location. Deer were loaded into a utility vehicle and transported to a portable central processing station. We estimated age via tooth replacement and wear (0.5–≥6.5 years old, Foley et al., 2021; Severinghaus, 1949), antler size (gross Boone & Crockett score; Wright & Nesbitt, 2003), total body length (in centimeters, tip of the nose to the base of the tail), and hind foot length (in centimeters, length between the posterior end of the tuber calcis and the hairline above the keratinized hoof). We also recorded body mass to the nearest 0.5 kg using an electronic platform scale. Because recruiting offspring is energetically costly and can influence the body mass of females (Rice, 2018), we also recorded lactation status. After recording all pertinent data, deer were released onsite. All capture methods followed the American Society of Mammalogists' guidelines (Sikes et al., 2019) and were approved by the Texas A&M University-Kingsville Institutional Animal Care and Use Committee (2011-10-01, 2014-09-29, 2017-09-22) and conducted under capture permits issued by the Texas Parks and Wildlife Department.

Phenotypes

Prior to testing hypotheses about drivers of deer phenotypes, we first conducted analyses to quantify phenotype size differences between sites, similar to those reported in

Rankins, DeYoung, Foley, et al. (2023) and Rankins, DeYoung, Wester, et al. (2023). Traits included antler size (males only), body mass, hind foot length, and total body length. Preliminary analyses based on von Bertalanffy growth curves indicated some departure from expected values for asymptotes in male antler size and body mass, possibly because of the influence of annual rainfall on these two traits (Foley et al., 2012, 2018) or not reaching an asymptote prior to ≥6.5 years old (Fuller et al., 1989). Mean values at maturity should be similar to asymptotes often presented with growth curves (Ricker, 1979); reporting the mean values reduces some of the errors that may occur with growth curves (Leberg et al., 1989). Therefore, we calculated the mean sex-specific trait value at ≥6.5 years old, after deer have completed physical maturity (Fuller et al., 1989; Gee et al., 2014; Hewitt et al., 2014; Strickland & Demarais, 2000). The difference between site-specific asymptotes and the mean trait size, excluding male antler size and body mass, was 0% ($n = 35$, range $= -1\%$ to 2%). Statistically different means were defined as nonoverlapping 95% CIs.

Factors influencing phenotypes

After calculating mean phenotype at maturity, we examined hypothesized causal factors, namely habitat characteristics. First, we created a spatially defined capture area to base our habitat analyses on. We used the pooled site-specific deer capture waypoints during 2011–2018 to create a 100% minimum convex polygon (MCP) for each site using ArcGIS (ESRI, Redlands, CA, USA). To account for deer movements as a result of the helicopter chases (Baumgardt et al., 2022; Northrup et al., 2014), we buffered each MCP by 400 m (the maximum chase distance reported by helicopter pilots). After buffering each MCP, we clipped each polygon by ranch boundaries because of a combination of potential hard edges such as the Gulf of Mexico, highways, 2.4-m woven-wire game fences, and poor deer habitat on adjacent properties.

Forage quality

We collected indices that represent variables we hypothesized to influence deer phenotype size (Table 1). Soil characteristics can affect vegetation quality (Jones et al., 2010); therefore, we used soil characteristics as a proxy for forage quality. We obtained three indices that may reflect forage quality: percent sandy loam, percent sand, and percent calcium carbonate ($CaCO_3$). Percent sandy loam was of interest because this soil type

has greater water retention, resulting in improved forage conditions for white-tailed deer in South Texas (McMahan & Inglis, 1974; Steuter & Wright, 1980). Relative to clay and loam, sand has low water retention, which limits the development of woody vegetation communities. Lastly, we collected data on $CaCO_3$ because calcium is important for bone and antler formation (Cain et al., 2019; Jones et al., 2010). We obtained soil data from the Natural Resources Conservation Service Web Soil Survey website (Soil Survey Staff, 2022). We extracted the value of each of these three metrics from a depth of 1–350 cm for each soil series within each clipped MCP. We chose a maximum depth of 350 cm because 90% of forbs, annuals, and succulents, which are more nutritious for deer than shrub foliage (Fulbright & Ortega-S, 2006), have root depths <350 cm (Schenk & Jackson, 2002). Finally, we weighted the three metrics of each soil series by surface area within each capture polygon, which provided a single value for each capture site.

Forage quantity

To measure vegetation quantity, we used Rangeland Analysis Platform (RAP, Jones et al., 2018, https://rangelands.app) to acquire annual vegetation quantity indices for each capture site (Table 1). Vegetation indices included the following: percent of capture site covered by perennial forbs and grasses, annual forbs and grasses, shrubs, and trees. The indices pertaining to percent of landscape covered by a plant type could hypothetically belong to either the forage quality or quantity category (Table 1). For instance, percent of annual forbs and grasses could belong in the quality category because annual forbs are highly nutritious but could also belong in the quantity category because the index is also related to abundance. Thus, we placed the percent cover indices into both the quality and quantity categories (Table 1).

We also obtained biomass (in kilograms per hectare) of perennial forbs and grasses and annual forbs and grasses for biologically relevant seasons. Precipitation in South Texas is variable, but bimodal in nature, and typically peaks in May and September (Fulbright & Ortega-S, 2006). Seasons were spring (March–May), spring–summer (March–Aug), and summer–autumn (June–September). The RAP estimates biomass values every 16 days; thus, biomass values were averaged for each of the three seasons. We validated whether perennial or annual forb and grass values derived from RAP reflect the actual biomass of preferred forbs that deer select. Fulbright et al. (2021) collected, dried, and

T A B L E 1   Site-specific habitat attributes collected for each deer capture site ($n = 7$) on four East Foundation ranches in South Texas, USA, during 2011–2018.

Attribute	Quality	Quantity	Value	Source
Sand (%)	X		Single	NRCS
Sandy loam (%)	X		Single	NRCS
CaCO$_3$ (%)	X		Single	NRCS
Perennial forbs + grass cover (%)	X	X	Annual	RAP
Shrub cover (%)	X	X	Annual	RAP
Tree cover (%)	X	X	Annual	RAP
Perennial forbs + grass biomass (kg/ha)		X	Annual	RAP

Note: "X" indicates whether habitat attributes could support the forage quality or quantity hypothesis explaining differences in white-tailed deer morphology.
Abbreviations: NRCS, Natural Resources Conservation Service; RAP, Rangeland Analysis Platform.

measured standing crop of forb species preferred by deer from six 2500-ha sites within our study area during 2011–2019. Grasses were not considered because they are relatively unimportant to deer diets (Hines, 2016). The six biomass sampling sites overlapped with six of our seven deer capture MCP; San Antonio Viejo-W was the lone exception where actual forb biomass was not measured. Standing crop of selected forbs were collected from fifty 0.5 × 0.5-m sampling frames on each of the six sites during September and October 2012–2019 (Fulbright et al., 2021); we used nonparametric correlations and linear regressions to compare the empirical data and RAP values collected during the same temporal period. Fulbright et al. (2021) also measured biomass of selected forbs inside grazing exclusion cages. However, we wanted to measure standing crop of selected forbs, which is an important consideration given the variation in cattle stocking rates and densities of nilgai antelope, a large (100–300 kg) intermediate feeder (Hines, 2016), on the four ranches (Fulbright et al., 2021; Peterson et al., 2020).

Rainfall

It is critical to quantify rainfall because the high variation creates a pulsed-resource environment with a strong link between forage and deer productivity metrics, such as fawn:doe ratios, body mass, and antler size (DeYoung et al., 2019; Foley et al., 2012, 2018). Further, average rainfall is greater and more consistent in coastal areas than in inland (Lawrence & Lopes, 2016). We used the centroid of each capture site to obtain monthly rainfall totals at a 4-km scale via PRISM (PRISM Climate Group, 2022) and summed rainfall values (in centimeters) for each of the three biologically relevant seasons established in the *Forage quantity* section.

Statistical analyses

Accuracy of ages estimated using the tooth wear method declines as deer become older (Foley et al., 2021); we adjusted ages of recaptured individuals as necessary based on age at first capture. After removing apparent age or phenotype measurement errors (<1%) from the dataset, we developed a set of candidate mixed-effects linear regression models for each sex-specific trait of interest (body mass, antler size, hind foot length, and total body length). Models for hind foot length and total body length represent skeletal size and should not be sensitive to annual precipitation (Suttie & Mitchell, 1983). Therefore, we included rainfall as an explanatory variable only for body mass and antler size, traits that fluctuate annually due to forage quality or quantity. Because of multicollinearity, a model for body mass and antler size had either (1) a habitat attribute value, (2) rainfall, or (3) an interaction between a habitat attribute and rainfall. Each model had estimated age treated as a categorical random effect. In the models for female body mass, we included lactation status (lactating or not) and we examined two separate interactions: an interaction between rainfall and habitat attributes, and an interaction between rainfall and lactation status. We used this approach because the effect of rainfall on lactation status (i.e., body mass) may depend on habitat attributes. All predictors were standardized to have a mean of 0 and SD of 1. We used Akaike information criterion (AIC) to select the top models; ΔAIC < 2.00 were considered to be competing models (Burnham et al., 2011). Focusing on only the top models can obscure the overall effects of other tested variables. Thus, we also examined the slope of each habitat attribute, after controlling for rainfall, to determine whether there was support for the forb quality versus quantity hypothesis. We conducted all analyses in R (version 3.6.0; R Core Team, 2020) using packages lme4 (Bates et al., 2015) and AICcmodavg (Mazerolle, 2020).

RESULTS

Phenotypes

During 2011–2018, we captured and measured the phenotype size of 1909 males and 2645 females from the seven capture sites (Table 2). Antler size was similar between El Sauz and Buena Vista; El Sauz had smaller antler size than all of San Antonio Viejo and Santa Rosa, whereas Buena Vista was smaller than all of San Antonio Viejo but not Santa Rosa (Figure 4). El Sauz males and females had shorter foot lengths than the other six capture sites. The body mass of males was similar to the pattern seen in antler size, whereas both El Sauz and Buena Vista females had lighter body mass than the other five sites. The total body length of both sexes was relatively variable, with deer from El Sauz being shorter than deer from most sites. Overall, El Sauz consistently had the smaller phenotypes; compared with the other sites, male antler size was 2.2%–9.8% smaller, male body mass was 10.0%–17.6% lighter, male foot length was 1.8%–4.1% shorter, male body length was 1.4%–5.8% shorter, female body mass was 1.4%–10.7% lighter, female foot length was 2.0%–3.2% shorter, and female body length was 0.9%–3.8% shorter.

Factors influencing phenotypes

Original MCP sizes, prior to clipping, averaged 5548 ha (range = 3765–8212 ha). Clipping MCP by ranch boundaries removed an average of 5% (range = 0%–10.9%) of the original capture MCP area ($\bar{x}$ = 5298 ha, range = 3496–8212 ha).

September and October RAP-based biomass values of both perennial and annual forbs and grasses were positively correlated with standing crop of selected forbs (Appendix S1: Figure S1). We performed linear regressions to determine which RAP-based biomass indices were more correlated with standing crop of selected forbs. Biomass of the standing crop of selected forage was not normally distributed (Shapiro–Wilk's test $p = <0.01$); we employed a natural log transformation, which satisfied the assumption of normality prior to conducting linear regressions. Biomass of perennial forbs and grasses explained more of the variation in standing crop of selected forbs than did biomass of annual forbs and grasses ($R^2 = 0.34$, $p = <0.01$ vs. $R^2 = 0.10$, $p = 0.02$, respectively; Appendix S1: Figure S2). Therefore, we used the RAP-based biomass of perennial forbs and grasses as an index of biomass of standing crop of selected forbs; annual forbs and grasses were excluded from further analyses.

Correlations between habitat attributes, soil characteristics, and rainfall ranged from −0.81 to 0.98 (Figure 5). Of note, percent sand was negatively correlated with percent shrub and percent sandy loam. Percent sandy loam was positively correlated with percent $CaCO_3$ and percent shrub. Additionally, both perennial forb and grass cover (in percentage) and perennial forb and grass biomass were positively correlated with

TABLE 2 Sex- and age-specific sample size of white-tailed deer captured on seven sites in South Texas, USA, during 2011–2018.

| Site | Sex | Age (years) | | | | | | | Total |
		0.5	1.5	2.5	3.5	4.5	5.5	≥6.5	
ES	F	73	73	54	64	71	87	270	692
BV	F	41	33	59	70	61	43	133	444
SR	F	28	40	37	35	50	66	136	393
SAV-E	F	28	28	38	50	52	56	149	402
SAV-N	F	27	39	37	42	38	29	113	326
SAV-S	F	14	18	29	28	19	29	104	241
SAV-W	F	8	12	18	21	9	18	61	147
ES	M	54	79	44	42	46	38	125	428
BV	M	30	42	51	49	48	52	92	364
SR	M	26	32	17	41	10	21	45	192
SAV-E	M	20	51	25	33	23	28	66	246
SAV-N	M	28	31	32	45	60	42	158	396
SAV-S	M	8	15	29	27	17	23	64	183
SAV-W	M	7	16	15	12	11	6	33	100

Abbreviations: BV, Buena Vista; ES, El Sauz; SAV, San Antonio Viejo; SR, Santa Rosa.
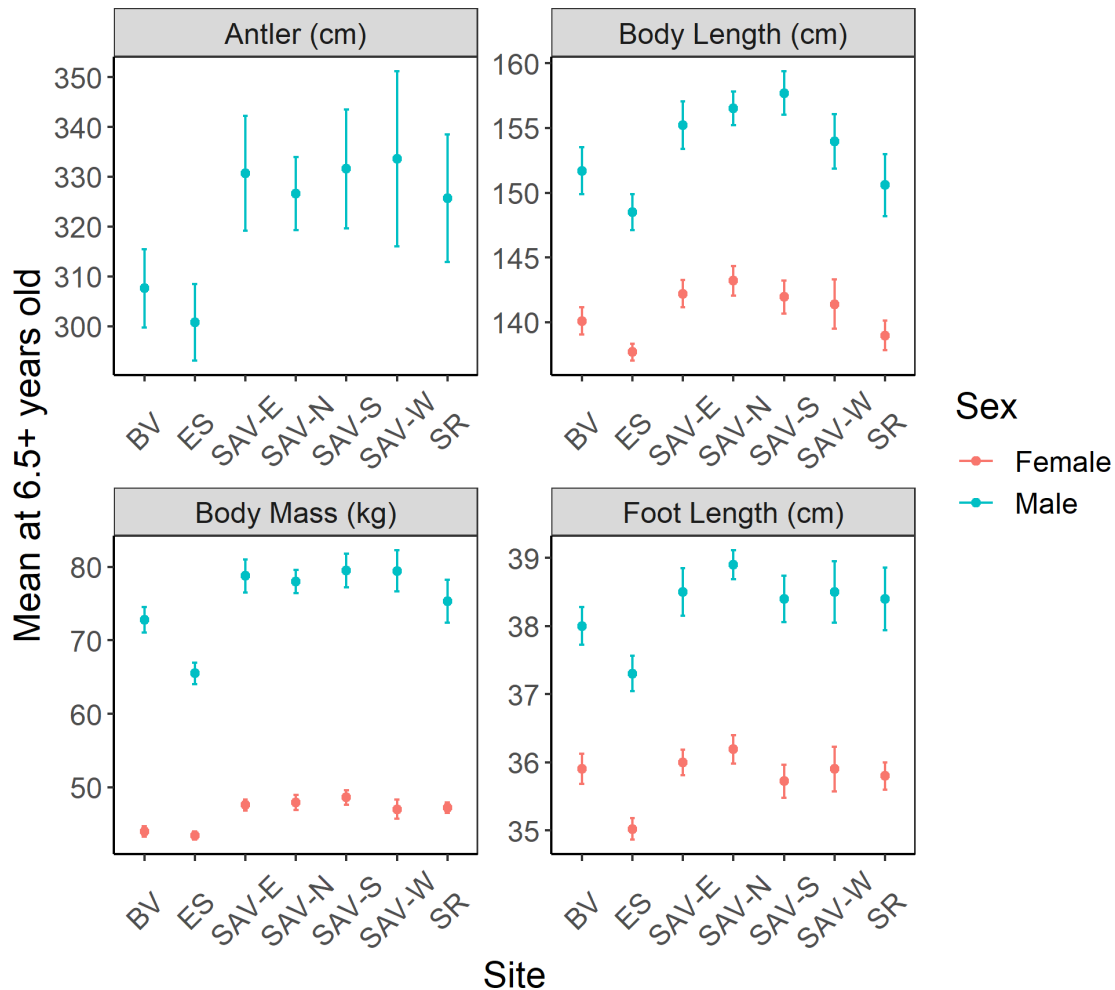
FIGURE 4 Mean values at physical maturity (≥6.5 years old) for antler size, body length, body mass, and foot length in male and female white-tailed deer captured on seven sites in South Texas, USA, during 2011–2018. Error bars indicate 95% CIs. BV, Buena Vista; ES, El Sauz; SAV, San Antonio Viejo; SR, Santa Rosa.
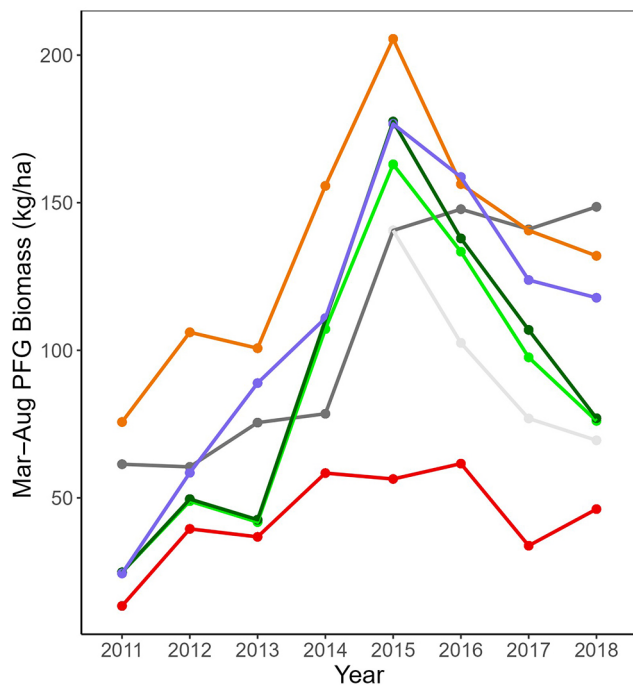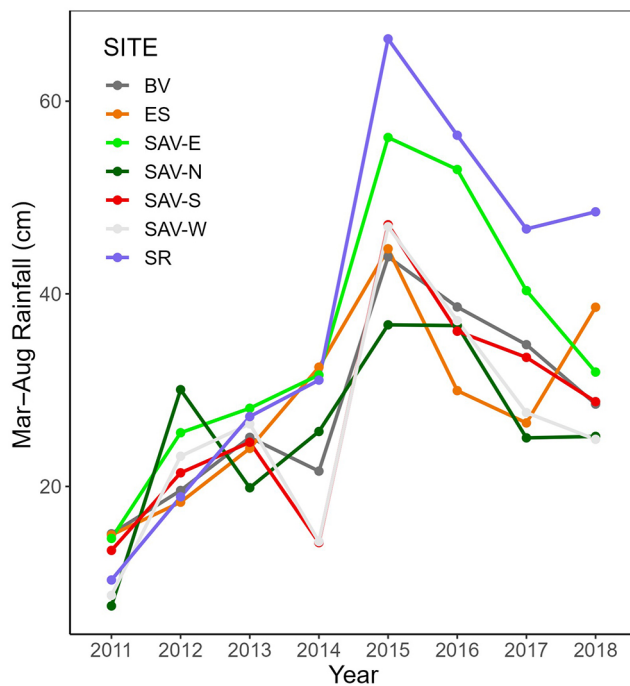
rainfall. Rainfall was variable and was lowest during 2011 (12 cm) and highest during 2015 (49 cm; Figure 6). El Sauz had the highest % sand (85.9%) and San Antonio Viejo-S had the lowest (58.7%; Figure 7). El Sauz had the highest average perennial forbs and grasses biomass during the 8 years (150.3 kg/ha, SD = 45.3) and San Antonio Viejo-S had the lowest average (48.5 kg/ha, SD = 17.9; Figures 6 and 7). San Antonio Viejo-S had the highest average shrub cover (48.1%), compared with Buena Vista (16.8%), El Sauz (17.3%), and San Antonio Viejo-N (18.3). San Antonio Viejo-S had the highest % sandy loam (85%) and CaCO₃ (12.4%), whereas Buena Vista had the lowest sandy loam (2%) and CaCO₃ (0.2%). All sites had <7% tree cover (mostly live oaks [*Quercus virginiana*]); El Sauz had the highest average (6.4%), and San Antonio Viejo-N had the lowest (1.8%).

Percent sand was the top-ranking model for skeletal size traits (Table 3). For every 7.7% increase in percent sand, male body length (−2.4 cm), male foot length

(−0.40 cm), female body length (−1.5 cm), and female foot length (−0.26 cm) declined. Percent sand and rainfall, including some interactions between these two variables, consisted of the top models for body mass and antler size (Table 3). The percent sand variable had a negative effect on all traits, whereas rainfall had a positive effect. For models with a significant interaction (antler size and male body mass), increases in rainfall dampened the negative effect of percent sand (Table 3). Although percent sand and rainfall were the dominant variables in all of our models, examination of whether slopes were significantly (p ≤ 0.05) positive or negative for the other habitat variables yielded a fairly consistent pattern. After controlling for rainfall by inclusion in the same models, percent sandy loam had a positive effect on all traits, whereas the effect of CaCO₃ was inconsistent (Table 4). Indices related to vegetation quality or quantity were consistently positive for percent shrubs and negative for percent cover of forbs. Further, each of the three
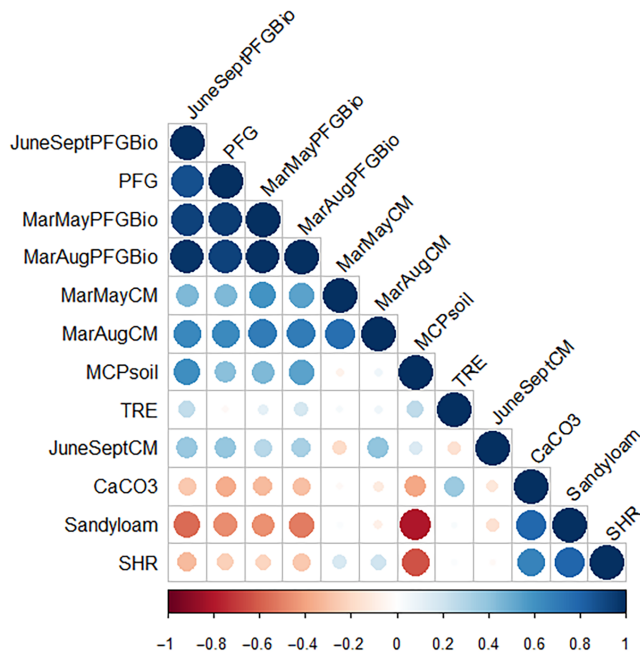
FIGURE 5 Pearson's correlation between environmental moisture values and habitat attributes from seven deer capture sites in South Texas, USA, during 2011–2018. CaCO₃, weighted % of calcium carbonate in the soil; CM, three seasonal values of rainfall in centimeters; MCP, minimum convex polygon; MCPsoil, weighted percentage of soil consisting of sand within a capture site; PFG, percent of perennial forbs and grass cover; PFGBio, three seasonal values of biomass of perennial forbs and grasses; Sandyloam, weighted percentage of soil classified as sandy loam within a capture site; SHR, percent of shrub cover; TRE, percent of tree cover.

seasonal indices for standing crop of forbs had negative slopes for each trait.

DISCUSSION

We found strong, but at times unexpected, associations between site characteristics and phenotypic traits. Overall, percent sand had the greatest influence on each phenotypic trait, likely mediated via effects on the vegetation community. Sand has lower water retention rates compared with clay and loam and thus poorer abilities to support woody plants. The soil-vegetation type association was evidenced by the negative correlation between percent sand and percent shrub cover and the positive correlation of percent sand with percent forb cover and standing crop of forbs. While sandy loam soils were not the dominant variable in our models, sandy loam consistently had a positive effect on each phenotypic trait size. Sandy loam soils were strongly correlated with percent shrub cover ($r = 0.79$). Trends in these two edaphic and vegetation characteristics (sand and forb vs. sandy loam and shrub) as it relates to phenotypic expression support our hypothesis that permanent soil conditions have a long-lasting effect on phenotype size (Jones et al., 2010; Strickland & Demarais, 2000).

Unexpectedly, all phenotypic traits were positively correlated with percent shrub cover rather than forbs.
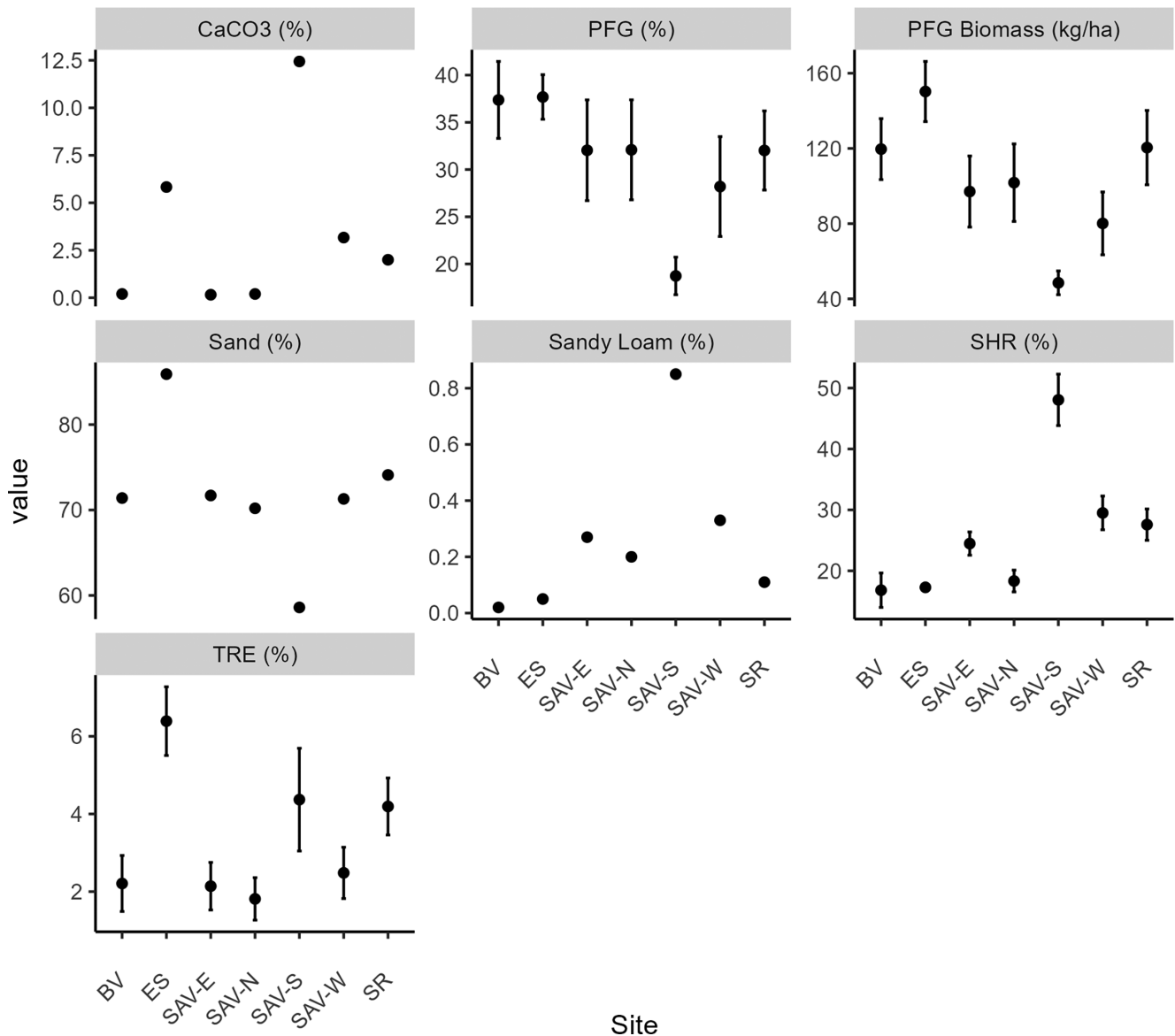

FIGURE 6 Rainfall and biomass of perennial forbs and grasses during March to August at seven white-tailed deer capture sites in South Texas, USA, during 2011–2018. Rainfall and biomass values were obtained from PRISM and Rangeland Analysis Platform, respectively. BV, Buena Vista; ES, El Sauz; PFG, perennial forb and grass cover; SAV, San Antonio Viejo; SR, Santa Rosa.

FIGURE 7 Habitat attribute values of seven sites where white-tailed deer were captured during 2011–2018 in South Texas, USA. CaCO₃, weighted % of calcium carbonate in the soil; PFG, percent of perennial forbs and grass cover, which was an index of selected forbs; PFG Biomass, biomass of perennial forbs and grasses (in kilograms per hectare), which was an index of selected forbs; Sand, weighted percentage of soil consisting of sand within a capture site; Sandy loam, weighted percentage of soil classified as sandy loam within a capture site; SHR, percent of shrub cover; TRE, percent of tree cover. BV, Buena Vista; ES, El Sauz; SAV, San Antonio Viejo; SR, Santa Rosa. Error bars indicate SEs.

For instance, El Sauz had on average 20%–68% greater forb biomass but had the smallest phenotype sizes for all traits. Conversely, San Antonio Viejo-S, which was among the sites with larger deer, had the greatest shrub cover (48%) and the least amount of forb biomass. The decline in phenotype size with increases in forb quantity was initially counterintuitive, as conventional wisdom is that forbs are the most important class of forage for white-tailed deer (Beasom & Scifres, 1977; Everitt & Gonzalez, 1981). However, that conventional wisdom was probably also influenced by the large influence of

rainfall on within-year productivity metrics such as body condition, lactation rates, fawn:doe ratios, and antler size (Foley et al., 2012, 2018; Ginnett & Young, 2000; Rice, 2018). Although forbs do represent the highest quality nutrition available in our semiarid system, they are highly ephemeral; forbs are abundant in wet years and virtually absent in dry years (Gann, Folks, et al., 2019; Gann, Fulbright, et al., 2019). Averaged across our study sites, variation in biomass of standing crop of forbs ranged from a low of 37 kg/ha (in 2011) to a high of 170 kg/ha (in 2015). Secondly, when sufficient rainfall

TABLE 3 Model statistics of top-ranking models (ΔAIC < 2.00) for seven sex-specific (M = male, F = female) white-tailed deer traits measured from seven capture sites in South Texas, USA, during 2011–2018.

Model	ΔAIC	AICcWt	Variable	1 SD	Range	Beta ± SE	95% CI	R^2_m	R^2_c
M-antler	0.00	1.00	Sand (%)	7.7	58.6–85.9	−9.83 ± 1.16	−12.11 to −7.56	0.02	0.80
			Mar–Aug rain (cm)	11.0	7.6–66.4	7.87 ± 1.14	5.64 to 10.11	...	...
			Sand × Mar–Aug rain[a]	...	...	−0.77 ± 1.38	−3.46 to 1.93	...	...
M-mass	0.00	1.00	Sand (%)	7.7	58.6–85.9	−3.48 ± 0.20	−3.86 to −3.09	0.03	0.86
			Jun–Sep rain (cm)	14.8	6.5–77.1	1.92 ± 0.20	1.53 to 2.30	...	...
			Sand × Jun–Sep rain	...	...	−0.61 ± 0.22	−1.05 to −0.17	...	...
M-foot	0.00	1.00	Sand (%)	7.7	58.6–85.9	−0.40 ± 0.03	−0.47 to −0.33	0.02	0.80
M-body	0.00	1.00	Sand (%)	7.7	58.6–85.9	−2.41 ± 0.19	−2.78 to −2.05	0.02	0.83
F-mass[b]	0.00	0.55	Sand (%)	7.7	58.6–85.9	−1.25 ± 0.10	−1.44 to −1.06	0.02	0.82
			Jun–Sep rain (cm)	14.8	6.5–77.1	0.92 ± 0.10	0.73 to 1.11	...	...
			Lactation (yes/no)	...	...	−1.64 ± 0.25	−2.12 to −1.15	...	...
			Sand × Jun–Sep rain[a]	...	...	−0.16 ± 0.11	−0.39 to 0.06	...	...
F-mass[c]	0.39	0.45	Sand (%)	7.7	58.6–85.9	−1.23 ± 0.10	−1.42 to −1.04	0.02	0.82
			Jun–Sep rain (cm)	14.8	6.5–77.1	0.93 ± 0.11	0.72 to 1.14	...	...
			Lactation (yes/no)	...	...	−1.62 ± 0.25	−2.11 to −1.13	...	...
			Lactation × Jun–Sep rain[a]	...	...	−0.08 ± 0.25	−0.57 to 0.40	...	...
F-foot	0.00	0.88	Sand (%)	7.7	58.6–85.9	−0.26 ± 0.03	−0.31 to −0.21	0.01	0.77
F-body	0.00	1.00	Sand (%)	7.7	58.6–85.9	−1.52 ± 0.13	−1.77 to −1.28	0.01	0.83

Note: Antler, antler size (in centimeters); mass, body mass (in kilograms); foot, hind foot length (in centimeters); body, total body length (in centimeters); range, observed range for the variable of interest; R^2_m, marginal R^2 associated with fixed effects only; R^2_c, conditional R^2 associated with fixed and random effects; sand, weighted percent of sand within capture site; lactation, whether females were lactating at capture (yes/no); PFG, biomass of perennial forbs and grass (in kilograms per hectare).
Abbreviation: AIC, Akaike information criterion.
[a]Not significant variable at $p = 0.05$.
[b]Top model for female body mass.
[c]Competing model for female body mass.

TABLE 4 Effect (P, positive; N, negative; NS, not significant at $p \leq 0.05$) of nine habitat variables on seven sex-specific traits (M, male; F, female) of white-tailed deer captured in South Texas, USA, during 2011–2018 after controlling for rainfall during Mar–Aug (and lactation status for female body mass).

	Quality (%)			Quality and quantity (%)			Quantity (kg/ha)		
Trait	Sand	Sandy loam	CaCO₃	PFG	Shrub	Tree	Mar–May PFGB	Mar–Aug PFGB	Jun–Sep PFGB
M-antler	N	P	NS	N	P	N	N	N	N
M-mass	N	P	NS	N	P	N	N	N	N
M-foot	N	P	N	N	P	N	N	N	N
M-body	N	P	NS	N	P	N	N	N	N
F-mass	N	P	NS	N	P	N	N	N	N
F-foot	N	P	N	N	P	N	N	N	N
F-body	N	P	N	N	P	N	N	N	N

Note: Habitat variables were grouped by support for forage quality hypothesis, forage quantity hypothesis, or both.
Abbreviations: PFG, perennial forb and grass cover; PFGB, perennial forb and grass biomass.

occurs, the standing crop of forbs produced by rainfall cannot be wholly consumed prior to plant senescence (Crider et al., 2015). Therefore, the erratic resource pulses provided by rainfall that create unusable surplus in standing crop of selected forbs cannot be a cause of the differences in phenotype sizes among sites.

Shrubs comprise most of white-tailed deer diets across seasons in southwestern Texas, particularly during autumn and early winter (Darr et al., 2019; Gann, Folks, et al., 2019; Gann, Fulbright, et al., 2019). During dry winters and springs when forbs are lacking, deer rely heavily on evergreen shrubs (Gann, Fulbright, et al., 2019). Furthermore, mast and flowers from shrubs are highly nutritious sources of energy and may comprise more than half of deer diets during summer (Folks et al., 2014; Gann, Folks, et al., 2019). Therefore, shrubs provide a more consistent source of forage availability throughout the year. This is critical because white-tailed deer are concentrate-selectors and have a wide diet breadth (DeYoung et al., 2019; Spalinger et al., 1986). White-tailed deer selectively forage a diverse array of highly nutritious plant parts instead of large amounts of low-quality forage (Fulbright & Ortega-S, 2006; Gann, Folks, et al., 2019). Because shrubs are a relatively permanent forage source and are largely independent of rainfall ($r = 0.04-0.20$), shrubs can act as a constant source of nutrition for continued investment toward skeletal growth.

While leaves and stems of shrubs are available for much of the year, the nutritional value of individual plants or species does change depending on growth state and mast production. However, the temporal asynchrony in phenology of forage species in a habitat with diverse plant communities allows for more consistent resource availability. If this reasoning is correct, an environment with diverse sources of forage should be productive habitat (Fulbright & Ortega-S, 2006; Holechek, 1984). Indeed, Rankins, DeYoung, Wester, et al. (2023) found evidence that the diversity of shrubs and cacti was higher in San Antonio Viejo-S (larger deer) than in El Sauz (smaller deer), which further suggests that forage diversity is a key to phenotype size in white-tailed deer in semiarid environments. Additional benefits of shrubs are that shrub clusters within grassland matrices have greater soil fertility than in intervening patches of grassland (Franco-Pizana et al., 1995). The ability of shrub clusters to support nutrient-rich soils may be another factor that positively affects phenotypic traits because of nutrient transfer to deer browsing on shrubs. Further, repeated browsing may increase the nutritional content of shrubs (du Toit et al., 1990). Compensatory growth in response to defoliation has been reported in many of the dominant shrubs important in deer diets (Fulbright et al., 2011; Gann et al., 2016; Teaschner & Fulbright, 2007). Finally, shrubs also offer readily accessible shade during summer, which may help maintain rates of forage intake by facilitating thermoregulation (Speakman & Krol, 2010; Wiemers et al., 2014).

The underlying cause of the relationship between abiotic and biotic factors causing geographical differences in phenotype size is resource availability (i.e., "resource rule hypothesis," McNab, 2010). The "resource rule" proposed by McNab (2010) suggests resource availability as the foundation of multiple ecological rules explaining geographical differences in phenotypic expression (Bergmann, 1847; Cope, 1887; Foster, 1964; Yom-Tov & Geffen, 2006). Shrubs provide the backbone of the "resource rule" because forbs are highly ephemeral in a pulsed environment (DeYoung et al., 2019). Limitations in resource availability can alter life history strategies (Stearns, 1989); individuals constrained by the environment may cease physical development at an earlier age to enable sufficient resources to devote toward reproduction (Strickland & Demarais, 2000). We observed this pattern visually with our dataset (Appendix S1: Figure S3); growth rates of each trait of deer in El Sauz, the site with the least amount of shrubs, appeared to slow down earlier in life than their counterparts, illustrating the impact of a constant resource availability (i.e., shrubs) on phenotypic expression.

Population processes, such as dispersal or density-mediated effects, are known to influence growth and survival, yet did not appear to influence our data. Males are the dispersing sex in white-tailed deer and may disperse up to 8.2 km from their natal range (McCoy et al., 2012). Therefore, one might expect greater variation in male response to environmental variables if their growth was influenced by conditions in the natal range prior to dispersal at 1.5–2.5 years of age. We observed a strong effect of fixed environmental variables on male skeletal traits. This suggests that either males did not disperse far enough to encounter other soil types or that the influence of the post-dispersal range on body growth is greater than that of the natal range. Males do not complete skeletal growth until after 4.5 years of age, so the post-dispersal range may be important in signaling when to cease investment in body size. Density-dependent effect on growth and survival (Bowyer et al., 2014; McCullough, 1999) rarely occur in pulsed environments because of the strong link between population performance (reproduction) and rainfall (DeYoung et al., 2019). Trends in population estimates (Figure 3) do not explain differences in phenotypic trait size because El Sauz had the smallest body size, albeit having 32%–44% lower deer density than the other three ranches. In addition, lactation rates varied substantially with rainfall, not population trends (Rice, 2018). Finally, minimal changes in deer density were observed even with the absence of recreational harvest, indicating that deer density did not appreciably change to the extent that resource availability would be impacted.

White-tailed deer are often managed for recreational harvest and deer managers need to understand that phenotype sizes are influenced by the environment, even at small spatial scales. Therefore, expectations, in terms of managing for certain phenotypic qualities, will depend on habitat characteristics (Strickland & Demarais, 2000). Improving deer habitat in rangelands such as ensuring availability of diverse shrub assemblages, assuming the soil type is compatible, will allow for resource availability during the frequent droughts associated with semiarid environments.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data (Foley, 2024) are available from Dryad: https://doi.org/10.5061/dryad.8931zcrzq.

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SUPPORTING INFORMATION

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