POPULATION PARAMETERS AND STRESS STATUS OF WHITE-TAILED DEER IN A VARIABLE SOUTH TEXAS ENVIRONMENT

A Thesis

by

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ABSTRACT

Population Parameters and Stress Status of White-tailed Deer in a Variable South Texas Environment

(August 2018)

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Ungulate populations experience a wide range of temporal and spatial environmental variation, especially in semiarid climates, which may influence the spatial use, condition, and fitness of white-tailed deer (*Odocoileus virginianus*). I captured deer on 4 study sites in South Texas to investigate the effects of environmental variation on white-tailed deer population parameters. I found a fine-scale pattern of nonrandom spatial association among fawns and adult females pooled across sites, suggesting a local population size about 3.5 – 4.5 km via Moran's *I* and Euclidean distance analysis. Females did not exhibit patterns of dispersal whereas males did, supporting the philopatric nature of females. Lactation patterns of white-tailed deer were strongly related to spring drought conditions in the semiarid region of South Texas. Mature females had a greater probability of lactation compared to juvenile females, and spring drought conditions had less influence on lactation probability of mature females compared to juveniles. Relationships between variable environmental conditions and population parameters have important implications for the sustainable management of white-tailed deer.

DEDICATION

I dedicate this thesis and my work throughout this project to my Lord and Savior. He gave me the strength I needed to finish this project with grace and humility. I thank Him for calling me to work with animals, His beloved creatures, and for blessing me with the company of the Holy Spirit along the way.

Secondly, I dedicate this thesis to my mother, Michelle Rice. She has encouraged me and supported me more than anyone in my life ever has. I want to thank her for always pushing me to do better, go farther, and be a more independent, loving woman. I have always been her little bird, and every day she gives me the courage to fly even farther.

Thirdly, I want to thank my family and “my village” for supporting me and encouraging me throughout my life. This includes my father, Mike, and my sister, Ciara. I want to thank my friends and lovely people I met along the way, including Matt and Jan Robinson. This work was not only about writing, but also about moving, adjusting, and growing. Included in my village are my professors and mentors from Gustavus Adolphus College. Thank you for challenging me, trusting me, encouraging me, and giving me the knowledge and freedom to take chances.

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CHAPTER I

POPULATION PARAMETERS OF WHITE-TAILED DEER IN A VARIABLE SOUTH TEXAS ENVIRONMENT

INTRODUCTION [1]

Wildlife populations are often delineated based on human constructs, including political or property boundaries, geographical origin, or phenotypic traits of individuals (Evanno et al. 2005). These boundaries do not usually reflect the social organization and genetic structure present in wildlife populations. Genetic structure refers to any spatial pattern of relatedness of individuals within a population. Genetic structuring occurs in most natural populations, even in populations of large and highly vagile organisms (Miller et al. 2010). Population boundaries may be obvious in patchy habitats, but determining these boundaries may be difficult in continuously distributed populations. Understanding genetic structure and population boundaries of species continuously distributed across the landscape is critical for effective local management.

The scale at which individuals are spatially dependent is greatly influenced by dispersal, a fundamental life-history process that enables individuals to cope with competition, inbreeding, and environmental stochasticity by maintaining heterozygosity (Bowler and Benton 2005). Dispersal can be influenced by social behavior of males and females, ecological and landscape barriers (i.e., resistance to gene flow), and resource availability (Honeycutt 2000). For many ungulates, including white-tailed deer (*Odocoileus virginianus*), dispersal is sex- and age-biased. Young males are the primary dispersers, whereas females are typically philopatric and establish home ranges that overlap with their mothers (Porter et al. 1991). Sex-biased dispersal can cause spatial

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genetic structuring to differ between males and females. A particular pattern of genetic structuring, isolation by distance (Wright 1943) occurs because individuals aggregated closely in space are more likely to be related than those at greater distances because dispersal distances are finite. Recently, studies of genetic structuring in ungulates have revealed genetic structure at much finer spatial scales than previously expected (Comer et al. 2005, Nussey et al. 2005). Fine-scale genetic structuring has implications for genetic diversity and thus the probability of inbreeding, disease transmission, and important evolutionary processes (Noble et al. 2016). These ecological phenomena should influence management practices and conservation decisions that rely on an understanding of genetic structuring and population biology.

Genetic structuring within and among populations can be illuminated through the quantification of genetic variation. Studies of relatedness, dispersal, and population structure have been revolutionized by availability of highly variable genetic markers, including microsatellites. Nuclear microsatellite DNA loci have been used to examine genetic variation, determine relationships among individuals, estimate gene flow patterns, and define population extent (Honeycutt 2000, Anderson et al. 2002). Microsatellites are ideal markers for describing such patterns due to their high mutation rates and subsequent high polymorphism (Honeycutt 2000). Sex-biased dispersal patterns, or non-random mating, can be assessed by contrasting sex-specific spatial patterns of spatial autocorrelation, under the assumption that increased philopatry by one sex causes greater genetic structure (Coltman et al. 2003, Peakall et al. 2003). The availability of highly informative genetic markers allows researchers to better understand population structure and extent, and barriers to gene flow in ungulates around the globe (Peakall et al. 2003).

The scale of genetic structuring is key to understanding the distribution of genetic variation within and among populations. The goal of my study was to describe and characterize the genetic structure of 4 unmanaged populations of white-tailed deer in South Texas using microsatellite markers. Specifically, among these 4 populations, my objectives were to: (1) quantify levels of genetic variability; (2) compare large-scale genetic differentiation between capture locations; (3) compare fine-scale genetic structure and spatial extent between fawns, adult females, and post-dispersal males; and (4) qualitatively describe dispersal distances of females and males as a mechanism driving genetic variability and structure.

STUDY AREA

My study was conducted on 4 ranches in the semiarid region of South Texas, USA, which encompass 84,530 ha of native Texas rangeland (Annala 2015). The study sites span a geographic area from the Gulf coast to 145 km inland (Fig. 1.1). These study sites are owned and operated as cattle ranches by the East Foundation. Wildlife is monitored but no explicit management or hunting of native wildlife occurs. All of the sites are surrounded by livestock fences (1.2 m in height), with portions of each ranch boundary containing taller fencing (2.5 m). Elevation ranges from 0 to 220 m following an east to west gradient (East Foundation 2016). The 4 sites lie within the Gulf Coastal Plains and South Texas Plains climate divisions. The Gulf Coastal Plains climate division is considered sub-tropical, while the South Texas Plains is sub-tropical humid (Texas Parks and Wildlife Department 2012). Annual average precipitation ranges from 46 to 61 cm and decreases along an east to west gradient (Fulbright et al. 1990, Texas Water Development Board 2012, East Foundation 2016). Variability in daily

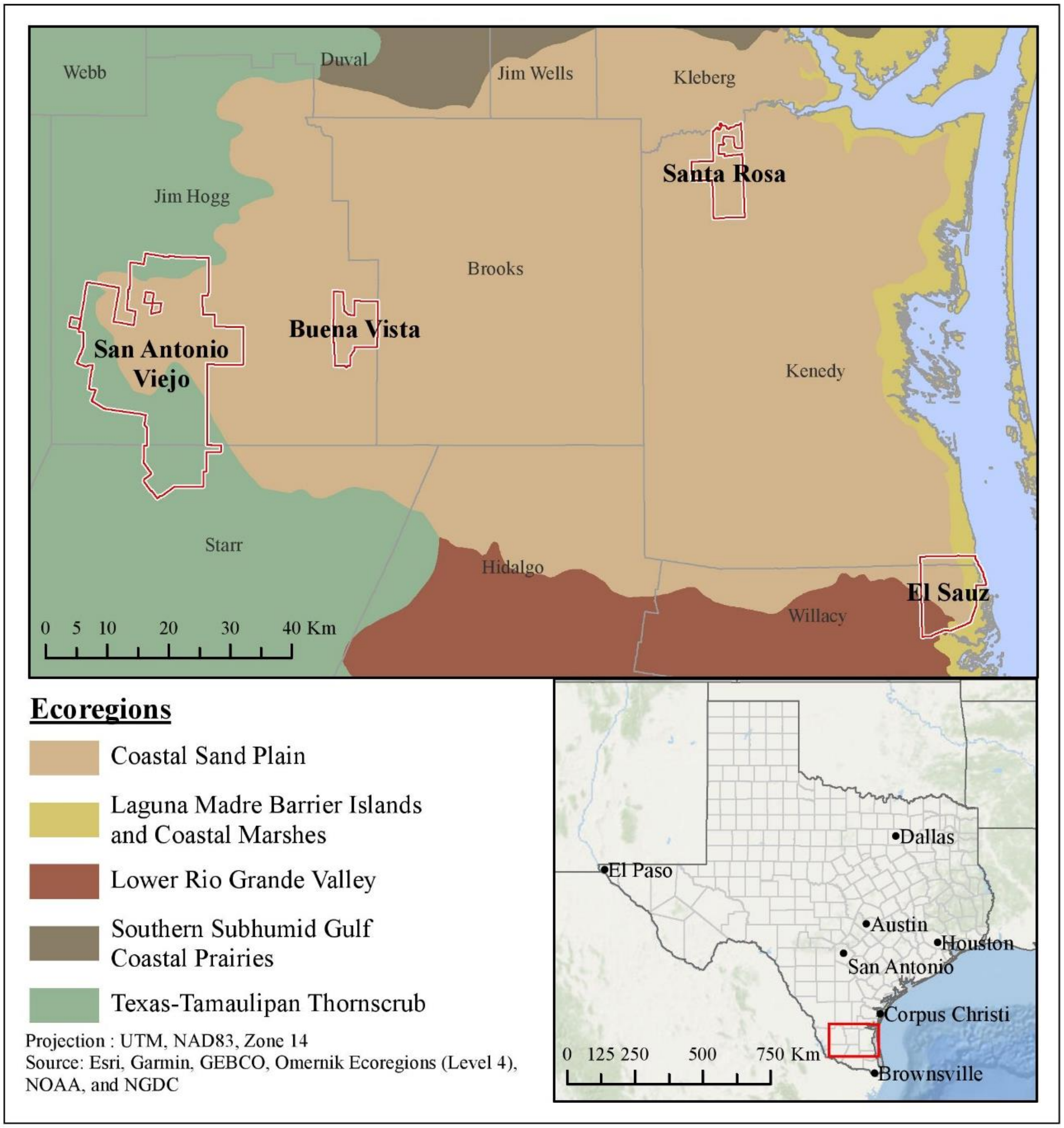

Figure 1.1. The East Foundation ranches, located in the South Texas Costal Sand Plain and Tamaulipan Thorn Scrub ecoregions.

temperature and precipitation increases inland away from the coast (Texas Parks and Wildlife Department 2012). The region experiences stochastic precipitation, with seasonal peaks in May – June and September – October. Precipitation is often low during November – March and modest in July – August (Fulbright et al. 1990, Texas Water Development Board 2012). September receives the highest monthly rainfall with an average of 11.9 cm (Texas A&M AgriLife Research and Extension Center 2015, Smith and Campbell 2017).

The 4 study sites occur in the Coastal Sand Plain and the Tamaulipan Thorn Scrub ecoregions. The Costal Sand Plain consists of grassland savannah interspersed with groves of woody vegetation dominated by live oak (*Quercus virginianus*) and honey mesquite (*Prosopis glandulosa*) groves, sand dunes, and saline habitats (Fulbright 1990). The Tamaulipan Thorn Scrub region consists of thicker thornscrub woodlands with a higher diversity of shrubs and forbs than the Coastal Sand Plain, primarily due to the higher fertility of soils (Hines 2016). The soils are acidic clays, clay loams, and caliche. Prominent species of vegetation are live oak, honey mesquite, brasil (*Condalia hookeri*), prickly pear (*Opuntia spp*), and spiny hackberry (*Celtis pallida*), all interspersed in grassland (Smith and Campbell 2017).

El Sauz, the easternmost and wettest property, is located along the Laguna Madre, near Port Mansfield in Kenedy and Willacy Counties, Texas, USA (lat 26°33’38.1 long -97°29’24.3). The property is in the Coastal Sand Plain ecoregion and consists of 11,201 ha of live-oak woodlands, upland dune topography, open grasslands, and salt marshes (Fulbright et al. 1990, Carr 2015). Precipitation is less variable due to periodic sea-breeze rains from the Gulf of Mexico. Aerial surveys conducted during November 2013 –

February 2015 suggested a density of white-tailed deer in this area ranged from 4.74 – 8.1 deer/km^2, which represents the lowest deer density of the 4 East Foundation properties (Annala 2015). Santa Rosa is 20 km south of Kingsville in Kenedy County, Texas (lat 27°10’33.0 long -97°50’59.3). This 7,471 ha property consists of a combination of Coastal Sand Plain woodland habitat dominated by live oak in sandy soil, and Tamaulipan Thorn Scrub and mesquite-huisache (*Acacia* f*arnesiana*) brush communities in heavier soils that developed in an abandoned pasture. Deer density ranged from 8.1 – 13.1 deer/km^2 (Annala 2015). Buena Vista is about 80 km south of Hebbronville in Jim Hogg County, Texas (lat 26°57’17.8 long -98°27’32.8). This 6,110 ha property consists of grassland savannah with widely spaced patches of woody vegetation spaced widely throughout. Deer densities ranged from 11.7 – 17.2 deer/km^2 (Annala 2015). San Antonio Viejo is about 60 km southwest of Hebbronville in Jim Hogg and Starr Counties, Texas (lat 26°54’20.5 long -98°36’34.7). This 57,011 ha property lies partially in the Coastal Sand Plain and the Tamaulipan Thorn Scrub ecoregions (Annala 2015). Most of the property is composed of Tamaulipan Thorn Scrub and grassland, but the eastern section is within the Coastal Sand Plain ecoregion, where the vegetation community consists of mesquite savannah with small live oak groves. Deer density across this study site ranged from 8.5 – 13.5 deer/km^2 (Annala 2015).

METHODS

Sample Collection

White-tailed deer were captured at random using a net gun deployed from a helicopter during 4 consecutive weekends in October and November in 2011 – 2016. Animals were restrained, fitted with a blindfold, and transported to a central processing site. The capture location of each animal was recorded using a handheld GPS unit. Coordinates were converted to UTMs for analysis. Individuals were aged according to tooth wear and replacement criteria (Severinghaus 1949) and placed into age classes ranging from fawn to ≥6.5 years old. I sexed individuals and marked them with numbered steel ear tags (National Band and Tag Company, New Port, KY), replacing missing or damaged tags as necessary. In 2015 – 2016, I obtained tissue biopsies (2 cm^2 in size) from the lower margin of the ear, using a livestock ear-notching tool. Samples were stored on ice in the field and frozen within 24 hrs. Individuals were released on site.

DNA Extraction and Amplification

I extracted DNA from ear tissue biopsies using a commercial kit (DNeasy Tissue kit, QIAGEN, Valencia, CA, USA) and followed the manufacturer’s protocol with a modified elution step; I eluted in 100 uL Buffer AE after an incubation of 10 min at room temperature. I amplified 15 microsatellite DNA loci via the polymerase chain reaction (PCR) from a panel described by Anderson et al. (2002). The microsatellite loci included INRA, Cervid1, ILSTS, N, Q, K, BL25, BM6438, O, BM848, BM6506, P, BM4208, D, and OarFCB193 (Anderson et al. 2002). Microsatellite loci were chosen based on previous performance in white-tailed deer genetic assays and paired in 8 multiplexed reaction mixes, following Anderson et al. (2002). The PCR products were combined with a denaturing mixture and size standard and loaded onto an 3130*xl* DNA sequencer (Thermo Fisher Scientific, Waltham, MA) for separation and detection. I scored allele calls and assembled multilocus genotypes using the computer program Gene Mapper (Thermo Fisher Scientific). If duplicate runs produced different allele calls, I did not score an allele for that particular locus. Individuals were excluded from the analysis if >40% of the genotypes were not able to be accurately scored.

Age Classes and Locations

I considered individuals that were initially captured at ≤1.5 years old as known-age. If an individual that was captured in 2015 – 2016 and successfully genotyped had a previous capture location that met the age class requirements, I used their first capture location that met these requirements. I used data from 2011 – 2014 to supplement missing capture locations from deer captured in 2015 – 2016. I used the first capture locations that met age class criteria to avoid sampling bias. Males that were captured as ≥2.5 year olds were categorized as post-dispersal males. Females that were captured as ≥1.5 year-olds were categorized as adult females. The female and fawn category was comprised of all aged females and fawns of both sexes.

Genetic Analysis

Genetic Diversity.– All analyses were performed using the computer program SPAGedDi, version 1.5 (Hardy and Vekemeans 2002). I calculated genetic diversity and departure from equilibrium expectations, including mean number of alleles, expected heterozygosity, observed heterozygosity, allelic richness, and F_{IS}. These measurements were calculated separately for all genotyped individuals, mature females, and mature males.

Genetic Structure.– To describe genetic structure over a larger scale across the landscape, I characterized genetic differentiation among the 4 sites. I calculated pairwise F_{ST} values for all pairs of locations based on Weir and Cockerham's (1984) F_{ST}. I assessed statistical support based on 10,000 permutations of gene copies among individuals.

To investigate and characterize fine-scale genetic structuring within sex and age classes, I performed an analysis of spatial autocorrelation (Miller et al. 2010). Specifically, I conducted autocorrelations for post-dispersal males, and female and fawns combined for sex-age classes for all sites combined and on the 4 study sites separately. Spatial autocorrelation analysis quantifies the relationship between genotype frequencies and Euclidean distance between individuals (Manel et al. 2003). I used Moran's *I* (Moran 1950), as a measure of autocorrelation for my analysis. Moran's *I* (averaged over loci) was taken for pairs of individuals separated by defined geographic intervals unique to each analysis. Each distance class had ≥100 pairs, to aid in the robustness of the analysis, except for the distance classes in the post-dispersal male analysis for Santa Rosa. I assessed statistical support for Moran's *I* based on 10,000 permutations of spatial group locations. I estimated standard errors by jack-knifing over loci.

Dispersal Estimates.– Male deer disperse from their natal area between 1 – 2 years of age. On a small scale, one might expect that pairs of close male relatives would be separated by greater spatial distances than distant relatives. Females may disperse from their natal area, but at much lower rates and distances, implying that females near one another on the landscape would be more closely related than those farther away. I calculated Queller and Goodnight's (1989) relatedness coefficient (*r*; range -1 to 1) for post-dispersal males and adult females to qualitatively assess the spatial distribution of close relatives. The relatedness estimator is an unbiased estimator of genetic relationships, quantifying the proportion of gene copies identical by descent. For example, expected *r* value for a parent-offspring pair is 0.5, half siblings is 0.25, and 1st cousins is 0.125. This estimator does not assume Hardy-Weinberg population allele frequencies (Queller and Goodnight 1989). I compared mean relatedness estimators to Euclidean distance to quantitatively compare patterns of relatedness between males and females among sites. To better understand male dispersal patterns, I compared positive relatedness values vs. Euclidean distance between pairs of post-dispersal males.

RESULTS

I genotyped 472 white-tailed deer captured across 4 sites during 2015 – 2016. This included 140 post-dispersal males (≥2.5 years old), 209 adult females (≥1.5 years old) and 74 fawns. Eighty percent of females captured from 2011 – 2016 were re-captured within 2 km of their initial capture site.

Genetic Diversity

The mean number of alleles per locus for all individuals (n = 472) was 14.3; the mean number of alleles per locus by capture location ranged from 9.5 (n = 61) to 12.7 (n = 207; Table 1.1). The Mean observed heterozygosity for all loci for all individuals was 0.73, ranged from 0.71 to 0.74 among capture locations, and was similar for all subclasses. The greatest F_{IS} measurement among capture locations was 0.12 at Buena Vista. Qualitatively, the properties with the greatest allelic richness values were El Sauz (10.1) and San Antonio Viejo (10.8). Genetic diversity was similar among sites for post-dispersal males, adult females, and all individuals. However, classes of deer on Santa Rosa had the lowest allelic richness and F_{IS} compared to the other properties.

Genetic Structure

Pairwise F_{ST} among sites ranged from 0.009 to 0.025, and all comparisons were statistically different from 0, indicating genetic differentiation between sites (Table 1.2).

Table 1.1. Sample size (*n*), mean number of alleles (*k*), expected heterozygosity (*He*), observed heterozygosity (*Ho*), allelic richness (*Ar*), and F_{IS} for white-tailed deer of all ages of males and females, post-dispersal males (≥2.5 years old), and adult females (≥1.5 years old) by site. Individuals were captured on 4 study sites in South Texas, USA. DNA samples were collected from captures that occurred during October – November 2015 – 2016. Genetic data were based on 15 DNA microsatellite loci.

Site	Class	*n*	*k*	*He*	*Ho*	*Ar*	F_{IS}
All	All	472	14.3	0.81	0.73	9.7	0.09
	Post-dispersal males	140	12.5	0.81	0.73	6.4	0.09
	Adult females	209	13.2	0.81	0.72	7.7	0.10
El Sauz	All	119	10.8	0.80	0.72	10.1	0.09
	Post-dispersal males	35	8.9	0.79	0.72	7.5	0.09
	Adult females	56	9.7	0.80	0.72	8.6	0.09
Santa Rosa	All	61	9.5	0.79	0.74	9.0	0.07
	Post-dispersal males	17	7.3	0.79	0.73	6.5	0.09
	Adult females	25	8.4	0.78	0.73	7.0	0.06
Buena Vista	All	86	11.1	0.80	0.71	9.4	0.12
	Post-dispersal males	32	9.2	0.80	0.70	6.4	0.14
	Adult females	35	9.3	0.80	0.73	7.3	0.09
San Antonio Viejo	All	207	12.7	0.79	0.73	10.8	0.08
	Post-dispersal males	67	11.0	0.80	0.77	9.0	0.05
	Adult females	100	11.8	0.79	0.71	9.2	0.10

Table 1.2. Pairwise F_{ST} values among all pairs of capture locations for white-tailed deer (*n* = 472) based on 15 microsatellite loci. Individuals were captured on 4 study sites in South Texas, USA. Captures occurred during October – November 2015 – 2016. Genetic data were based on 15 DNA microsatellite loci. All pairwise F_{ST} values are statistically significant from 0.

Ranch	El Sauz	Santa Rosa	Buena Vista
El Sauz			
Santa Rosa	0.024		
Buena Vista	0.019	0.02	
San Antonio Viejo	0.017	0.025	0.009

The San Antonio Viejo and Buena Vista pair had the lowest pairwise F_{ST} value, while San Antonio Viejo and Santa Rosa pair had the largest pairwise F_{ST} value. There was qualitative evidence for an overall isolation by distance pattern in that F_{ST} was positively correlated with geographic distance; however, all pairs that included Santa Rosa had higher pairwise F_{ST} values for the same geographic distance (Fig. 1.2). The San Antonio Viejo – El Sauz pair had a lower F_{ST} value than the San Antonio Viejo – Santa Rosa pair, although there was greater spatial distance between the San Antonio Viejo – El Sauz pair. For fine scale genetic analyses, I observed positive autocorrelation of Moran's *I* with Euclidean distance for fawns and mature females for all sites combined, with an intercept of about 3.5 – 4.5 km (Fig. 1.3). There was no spatial autocorrelation pattern observed for post-dispersal males (Fig 1.4). Significant autocorrelation values were more sporadic for males than females and fawns and there were no significant autocorrelation values after 3.5 km. Males in general had lower Moran's *I* values than females and fawns for the same distance class. Autocorrelations of mature females and fawns analyzed separately by study site exhibited less spatial autocorrelation patterns than fawns and mature females pooled across sites (Fig. 1.5). In the first distance class in El Sauz, there were 6 pairs of fawns and females, with the highest Moran's *I* value among all of the female and fawn autocorrelation analyses. Autocorrelation values were generally higher for fawns and mature females than for mature males (Fig. 1.6).

Dispersal Estimates

There was a negative linear relationship for mean estimated relatedness values and Euclidean distance for adult females at El Sauz ($P < 0.01$; Fig. 1.7). There was also a

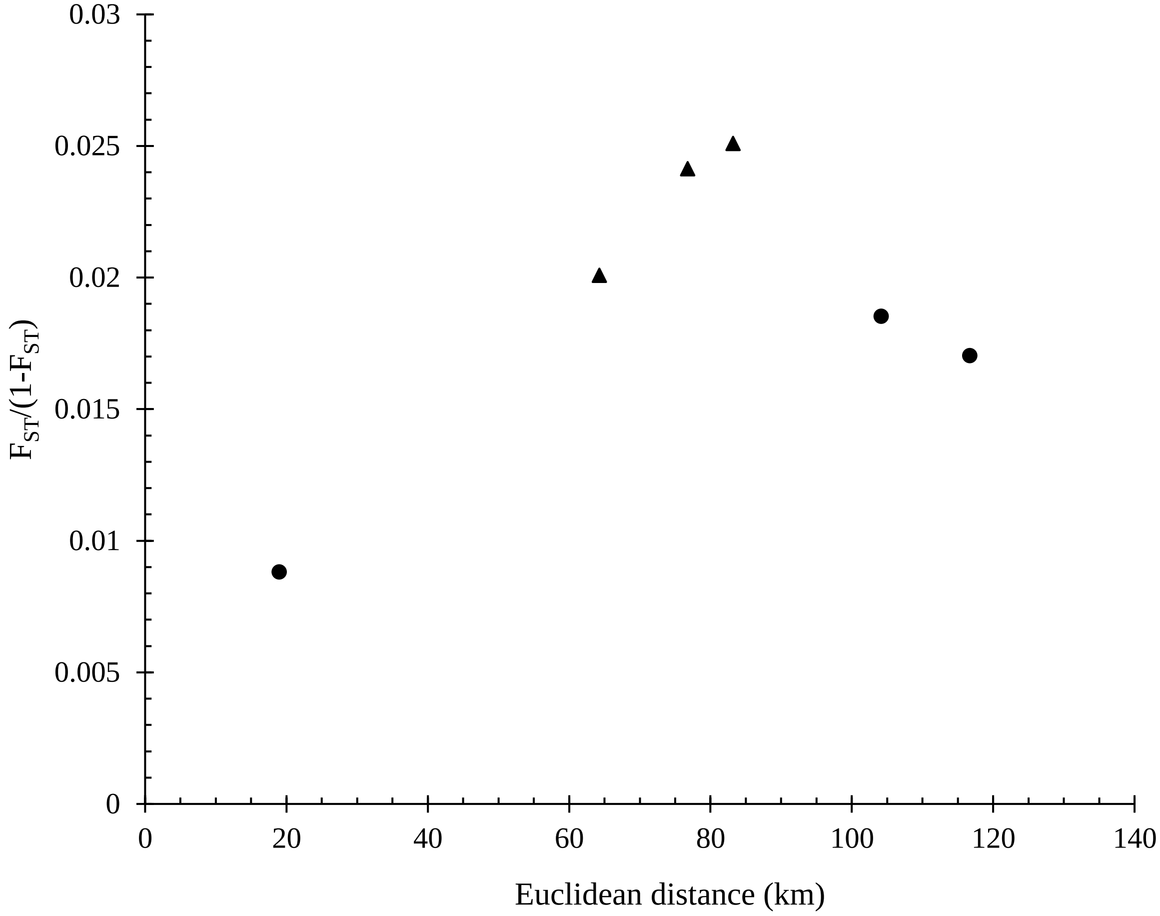

Figure 1.2. Linearized F_{ST} and Euclidean distance among pairs of 4 study sites. White-tailed deer (*n* = 472) were captured on 4 study sites in South Texas, USA. Captures occurred during October – November 2011 – 2016. Genetic data were based on 15 DNA microsatellite loci. Pairs including Santa Rosa are depicted with a triangle.

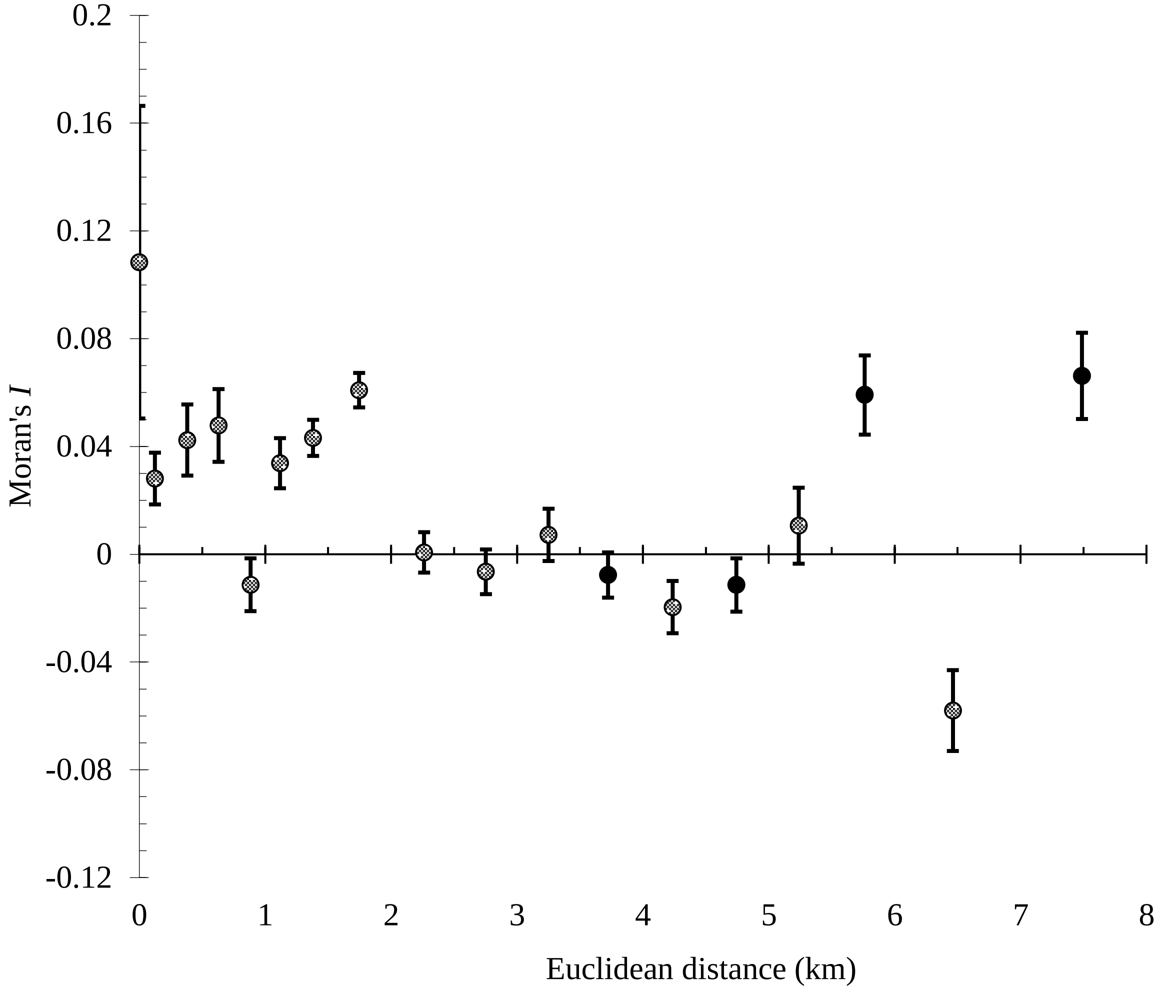

Figure 1.3. Mean autocorrelation coefficients (Moran's *I*) and Euclidean distance among pairs of fawns and adult female (≥1.5 years old) white-tailed deer (*n* = 251) in distance classes with >100 pairs. Intercept is about 3.5 – 4.5 km. Fawns and females were captured on 4 study sites in South Texas, USA. Captures occurred during October – November 2011 – 2016. Genetic data were based on 15 DNA microsatellite loci. Open points represent values significantly different than mean permutated values. Error bars indicate ±1 SE.

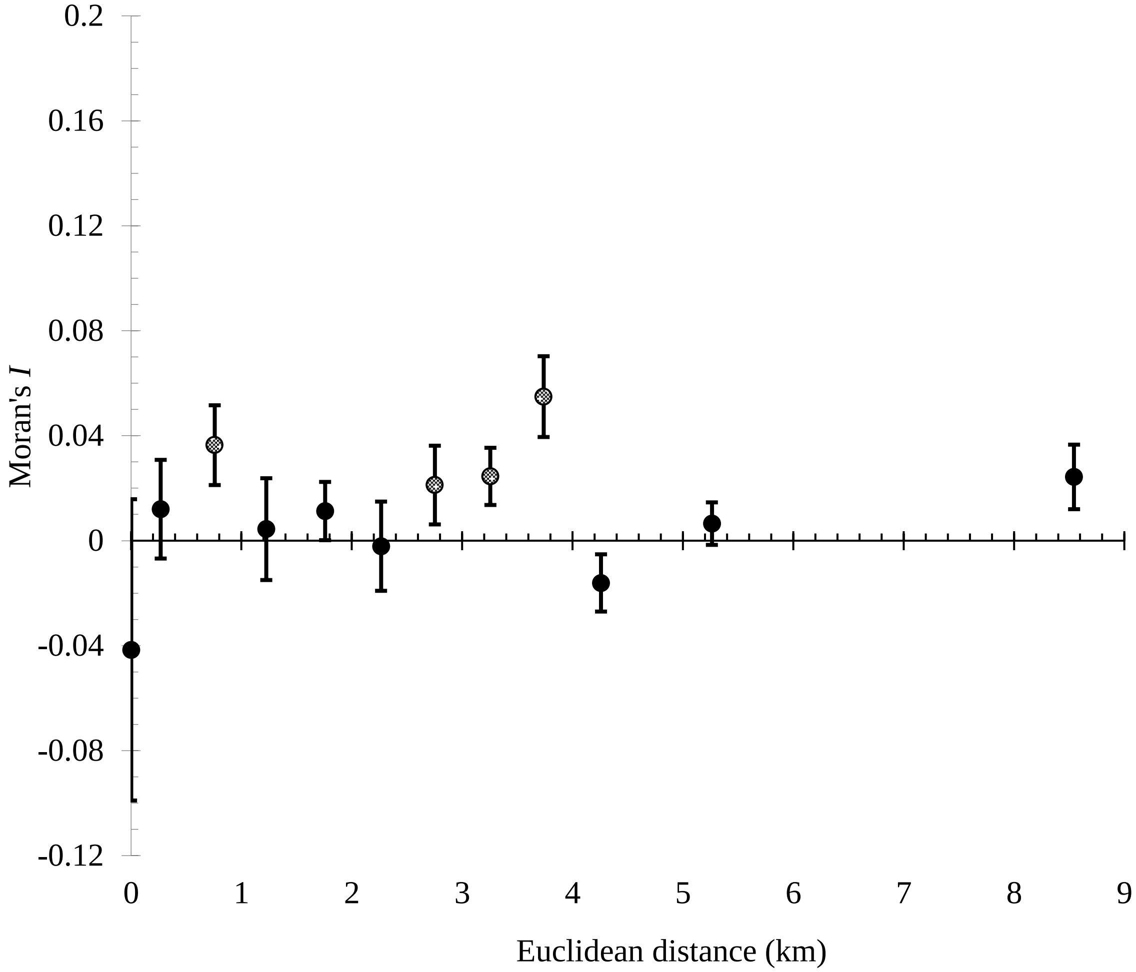

Figure 1.4. Mean autocorrelation coefficients (Moran's *I*) and Euclidean distance among pairs of post-dispersal (≥2.5 years old) male white-tailed deer (*n* = 140) in distance classes with at least 100 pairs. Males were captured on 4 study sites in South Texas, USA. Captures occurred during October – November 2011 – 2016. Genetic data were based on 15 DNA microsatellite loci. Open points represent values significantly different than mean permuted values. Error bars indicate ±1 SE.

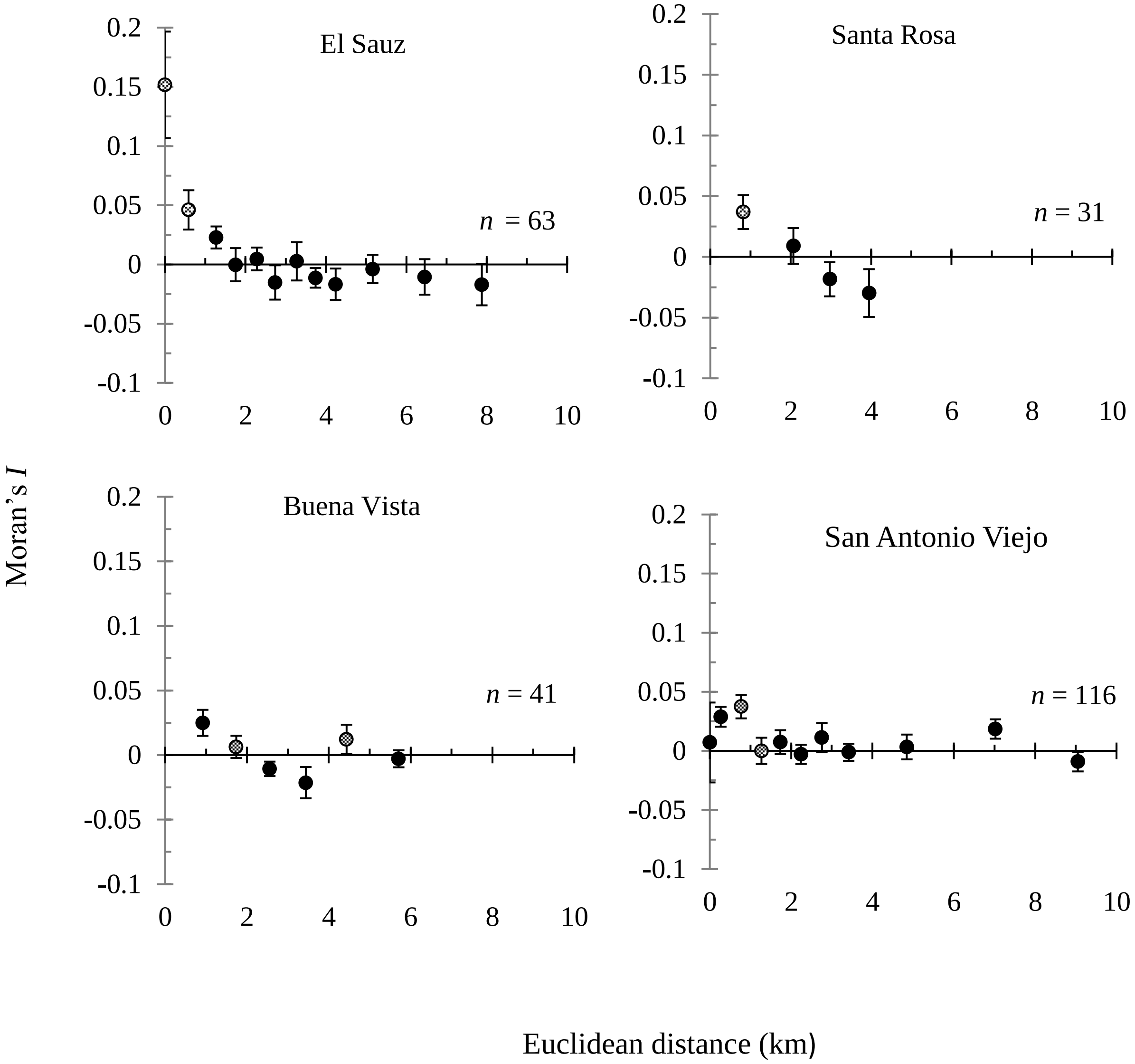

Figure 1.5. Mean autocorrelation coefficients (Moran's *I*) and Euclidean distance among pairs of fawns and adult (≥1.5 years old) female white-tailed deer in distance classes with at >100 pairs. Fawns and females were captured on 4 properties in South Texas, USA. Captures occurred in October and November of 2011 – 2016. Open points represent values significantly different than mean permuted values. Error bars indicate ±1 SE.

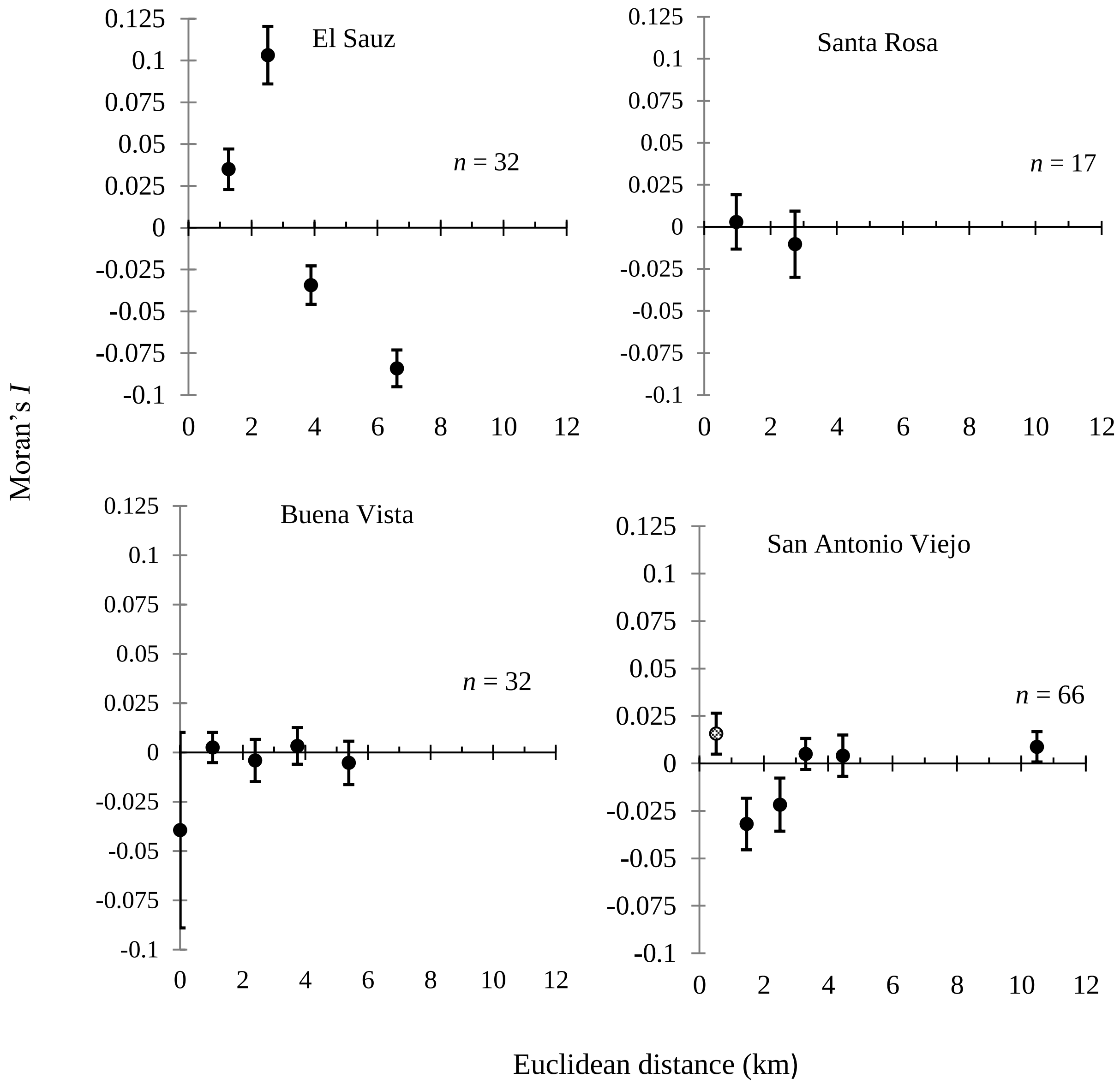

Figure 1.6. Mean autocorrelation coefficients (Moran's *I*) and Euclidean distance among pairs of post-dispersal male (≥2.5 years old) white-tailed deer. All distance classes, except for classes in Santa Rosa, had over 100 pairs. Number of pairs in Santa Rosa for the 2 distance classes were over 50. Males were captured on 4 study sites in South Texas, USA. Captures occurred during October – November 2011 – 2016. Genetic data were based on 15 DNA microsatellite loci. Open points represent values significantly different than mean permuted values. Error bars indicate ±1 SE.

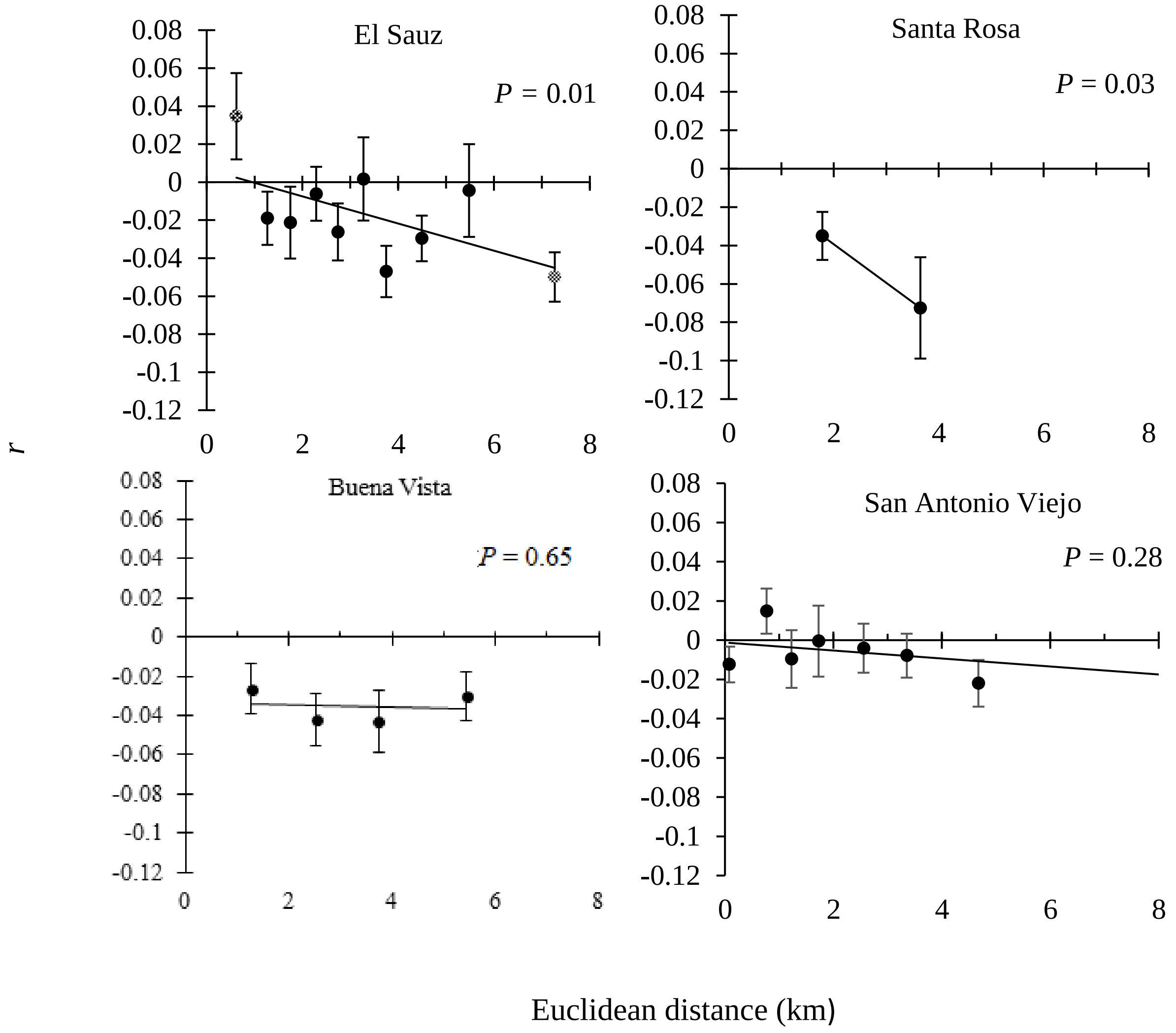

Figure 1.7. Mean estimated relatedness coefficients (*r;* Queller and Goodnight 1989) and Euclidean distance among pairs of adult (≥1.5 years old) female white-tailed deer. Females were captured on 4 study sites in South Texas, USA. Captures occurred during October – November 2011 – 2016. Genetic data were based on 15 DNA microsatellite loci. Open points represent values significantly different than mean permuted values. Error bars indicate ±1 SE.

significant negative linear relationship for adult females at Santa Rosa, although there were only 2 distance classes. There was no linear relationship for mean estimated relatedness values and Euclidean distance at Buena Vista ($P = 0.65$) or San Antonio Viejo ($P = 0.28$). Mean relatedness values were all negative for females on Buena Vista, although means were not statistically significant. Means were also not different than 0 for San Antonio Viejo. There were no linear relationships between estimated relatedness values and Euclidean distance for post-dispersal males on the 4 sites (Fig. 1.8). The greatest relatedness coefficients for post-dispersal male pairs among capture locations ranged from 0.68 (San Antonio Viejo) to 0.48 (Buena Vista; Fig. 1.9). Males at San Antonio Viejo had estimated relatedness coefficients of about 0.50 for up to 17 km, which represents the farthest pair of males with a relatedness coefficient of above 0.40. A pair of males at Santa Rosa had an estimated relatedness coefficient of approximately 0.50 around 4 km, representing the shortest distance for the last pair of highly related males captured on a property.

DISCUSSION

White-tailed deer are continuously distributed across the landscape, and thus it can be difficult to determine the appropriate spatial scale of management actions. I observed genetic structure and differentiation at both broad and fine scales among and between the 4 study sites. My results indicate that overall, the genetic variation among sites was similar, matching my prediction that genetic variation among capture locations would be low. Similar levels of genetic variation among sites may indicate movement of individuals between populations of white-tailed deer throughout the landscape, resulting in low levels of isolation between sites. Females exhibited fine-scale genetic structure

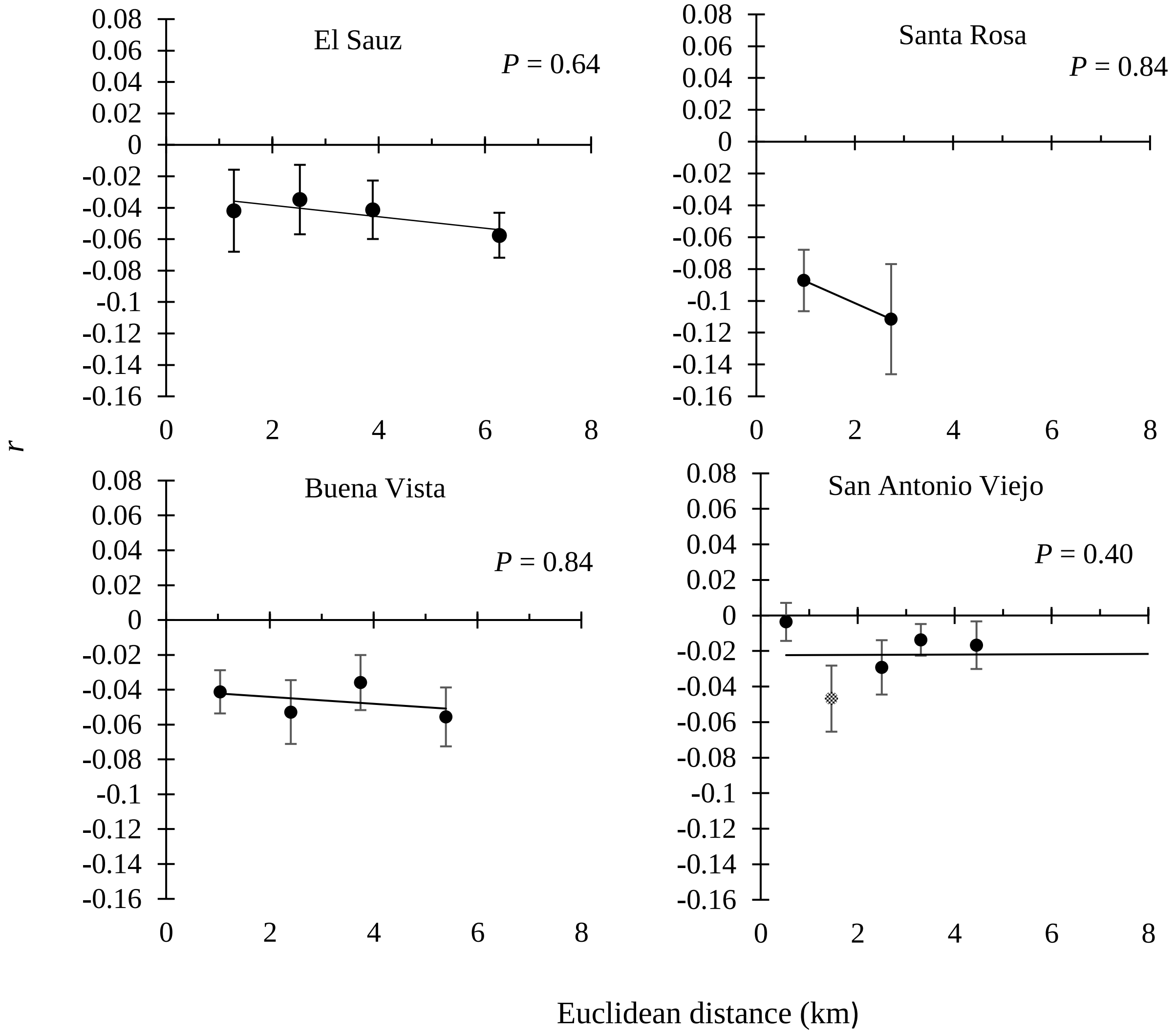

Figure 1.8. Mean estimated relatedness coefficients (*r;* Queller and Goodnight 1989) and Euclidean distance among pairs of post-dispersal (≥2.5 years old) male white-tailed deer. Males were captured on 4 study sites in South Texas. Captures occurred during October – November 2011 – 2016. Genetic data were based on 15 DNA microsatellite loci. Open points represent values significantly different than mean permuted values. Error bars indicate ±1 SE.

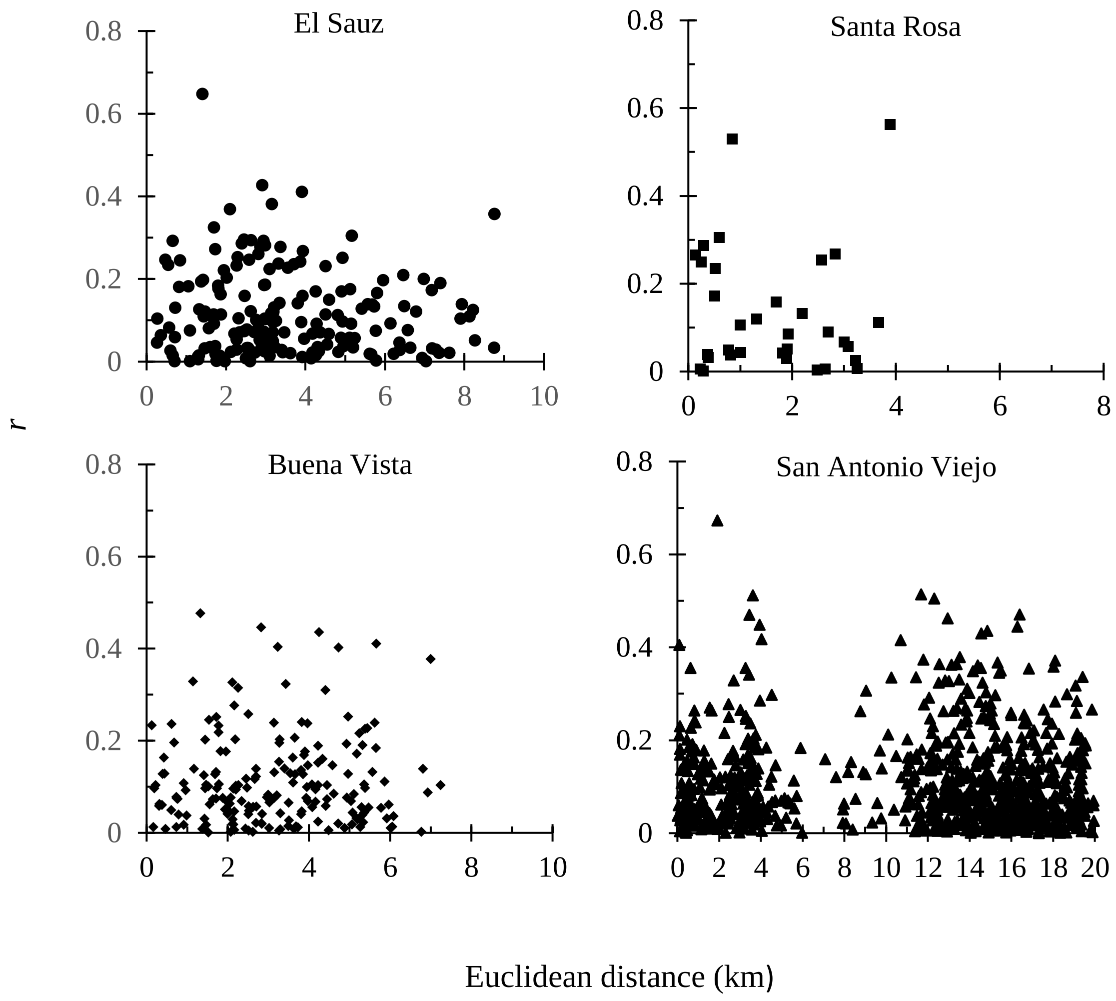

Figure 1.9. Estimated relatedness coefficients (*r;* Queller and Goodnight 1989) and Euclidean distance among pairs of post-dispersal (≥2.5 years old) male white-tailed deer.. Males were captured on 4 study sites in South Texas, USA. Captures occurred during October – November 2011 – 2016. Genetic data were based on 15 DNA microsatellite loci. Note that x-axes differ among sites.

whereas males did not, indicated by spatial autocorrelation patterns. Females did not exhibit patterns of dispersal whereas males did, supporting the philopatric nature of females.

Deer populations can exhibit genetic differentiation due to historic or modern resistance to gene flow. Although the 4 sites had similar levels of genetic diversity, the frequency and identity of alleles were different among sites, and there was a relative pattern of isolation by distance. Specifically, deer sampled on Santa Rosa had qualitatively lower allelic richness and F_{IS} compared to the other properties. Pairwise F_{ST} comparisons involving Santa Rosa also displayed greater differentiation than the other sites over the same geographic distance. This pattern of greater genetic differentiation and lower genetic diversity compared to other sites suggest that some demographic or historical factors differ for Santa Rosa compared to the other sites. Estimates of F_{ST} can be influenced by dispersal, mating systems, effective population size, or historic or modern restrictions to gene flow such as habitat loss or fragmentation (Nussey et al. 2005, Cullingham et al. 2010). Santa Rosa is closest to a large highway and to fragmented habitat to the east and west of the property. These anthropogenic disturbances may limit deer dispersal over time; however, my analyses cannot provide a definitive explanation for these patterns.

The difference in representation of alleles among sites may also play a minor role in the different body sizes, weights, and antler sizes (Gann 2016) observed in East Foundation deer among the 4 sites. Santa Rosa deer are typically larger in size and weight, with larger antlers compared to deer captured on El Sauz and Buena Vista. Although the physical differences among deer are mainly attributed to soil variability among sites and not genetic differentiation, variation in genetic diversity suggests potential differences in effective population size, or possibly dispersal patterns among sites. Clearly more research needs to be conducted to understand the relationship between population size, dispersal, and phenotypic traits.

I found a fine-scale pattern of nonrandom spatial association among fawns and adult females pooled across sites. The nonrandom spatial patterns found in this analysis meet the prediction that philopatric white-tailed deer female would exhibit fine-scale structure. For females and fawns pooled across sites, the intercept of this analysis was about 3.5 km, or a spatial area of about 4.9 km^2 (490 ha). Miller et al. (2010) observed that home-range sizes of females positively correlated with the extent of spatial autocorrelation. The spatial scale of structure for females captured in South Texas was larger than observed in a high-density population in West Virginia, where the intercept was about 1 km (Miller et al. 2010). The fine-scale structuring was a function of social groups composed of related individuals (Miller et al. 2010). Social structure and fine-scaled genetic structure have been observed in female red deer (*Cervus elaphus*; Nussey et al. 2005) and white-tailed deer (Cullingham et al. 2010), which suggests that many females also remained philopatric in these cervid populations.

Resources in the semiarid region of South Texas are far more spread out than more temperate regions. Fine-scale structure may be related to habitat distribution and quality and behavioral responses (Miller et al. 2010). Deer in South Texas may thus require a larger home range and familial groups may potentially share a spatial range, lessening fine-scale structure.

Spatial autocorrelation patterns were less distinct for fawns and females per site. Analysis per capture location was more limited by sample size than females and fawns pooled across sites. Although many Moran's *I* values per distance class were not statistically different than the mean permuted values, similar trends in spatial autocorrelation trends were still present. Variation in fine-scale structure among sites may be due to differences in resources among sites, soil communities, and vegetative communities (Gann 2016). The variation in resources may influence home-range size which can influence the spatial scale of genetic structure, which is why the extent of fine-scale structure might vary extensively throughout the range of white-tailed deer (Miller et al. 2010).

There was a negative linear relationship for mean estimated relatedness values and Euclidean distance for adult females on El Sauz. There was also a significant negative linear relationship for adult females on Santa Rosa, although there were only 2 distance classes. There was no linear relationship for mean estimated relatedness values and Euclidean distance on the other 2 capture locations. Since females are primarily philopatric, I predicted mean relatedness to significantly decrease after 3.5 – 4.5 km, which corresponds to the approximate spatial area of fawn and female populations across the capture locations. The scale of the analysis may not have been fine-scale enough to detect differences in relatedness in distances under 2 km since mean relatedness values for females after about 1 km were generally negative, indicating less relatedness than a fawn or female pair presented at random.

Post-dispersal males did not exhibit autocorrelation patterns pooled across sites or by capture location. This is expected of sex-biased dispersal, especially in relatively open habitats as males are less restricted to dispersal as they distribute themselves to maximize access to mates (Rosenberry et al. 2001, Campbell et al. 2005, Long et al. 2005). Yearling males on 2 study sites in South Texas dispersed at rates of 44% and 68%, with distances of 4.4 ±1.0 km and 8.2 ±4.3 km respectively (McCoy et al. 2005), which corresponds to the relatedness values observed from 4 – 8 km across the 4 sites.

There was also no linear relationship between mean estimated relatedness values and Euclidean distance for post-dispersal males among capture locations. In addition, there were relatively large relatedness coefficients at larger spatial distances, especially on San Antonio Viejo, which may reflect the larger sampling are covered at this site.

Due to the nature of this study, errors in spatial coordinates for individuals are inherent, however mistakes in spatial coordinates can only weaken spatial structure in the analysis, not create spatial structure where none exists. In addition, autocorrelation analysis counts for some variability due to distance classes (Miller et al. 2010). It is also sensible to conclude that the location where individuals were captured by the helicopter are reasonable spatial locations since 80% of females captured later were re-captured within 2 km of their initial capture site.

White-tailed deer are an economically and ecologically important species in Texas (Comer et al. 2005). In addition, populations are often highly managed in the rangelands of Texas. Most properties in Texas are small relative to the scale at which deer use the landscape, even in South Texas, where property sizes tend to be larger than other parts of the state (McCoy et al. 2005). Understanding spatial extent of males and females can be used to inform managers about the scale of their management practices in comparison to actual population extent of deer. This study is especially important because it can provide a baseline understanding of genetic structure across South Texas for unmanaged and unhunted deer populations. Effects of intense harvest of males and females on dispersal and group dynamics of cervids around the world is important for future research and management (Miller et al. 2010).

Finally, understanding deer dispersal movements and spatial extent is crucial for predicting spread of diseases including chronic wasting disease. Population genetics provides tools to study factors affecting disease spread where gene flow can be used as a proxy for the movement of infectious individuals (Cullingham et al. 2010). Low genetic differentiation may suggest that diseases have the potential to spread across a large spatial area over the long-term via dispersal (Cullingham et al. 2010). Genetic discontinuities among subpopulations may lead to knowledge of landscape barriers.

LITERATURE CITED

Anderson, J. D., R. L. Honeycutt, R. A. Gonzales, K. L. Gee, L. C. Skow, R. L. Gallagher, D. A. Honeycutt and R. W. DeYoung. 2002. Development of microsatellite DNA markers for the automated genetic characterization if white-tailed deer populations. Journal of Wildlife Management 66:67–74.

Annala, M. 2015. Using mark-recapture distance sampling in aerial surveys of large mammals in South Texas. Thesis, Texas A&M University-Kingsville, Kingsville, USA.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behavior to spatial dynamics. Biological Reviews of the Cambrige Philosophical Society 80:205–225.

Campbell, T. A., B. R. Laseter, W. M. Ford, and K. V. Miller. 2005. Population characteristics of a central Appalachian white-tailed deer herd. Wildlife Society Bulletin 33:212–221.

Carr, W. R. 2015. Plants of the South Texas Sand Sheet home. Biosci.utexas.edu. <http://www.bio sci.utexas.edu/prc/digflora/wrc/carr-sandsheet.html>. Accessed 4 Oct 2015.

Coltman, D. W., J. G. Pilkington, and J. M. Pemberton. 2003. Fine-scale genetic structure in a free-living ungulate population. Molecular Ecology 12:733–742.

Comer, C. E., J. C. Kilgo, G. D’Angelo, T. C. Glenn, and K. V. Miller. 2005. Fine-scale genetic structure and social organization in female white-tailed deer. Journal of Wildlife Management 69:332–344.

Cullingham, C. I., E. H. Merrill, M. J. Pybus, T. K. Bollinger, G. A. Wilson, and D. W. Coltman. 2010. Broad and fine-scale genetic analysis of white-tailed deer populations: estimating the relative risk of chronic wasting disease spread. Evolutionary Applications 4:116–131.

East Foundation. 2016. Our land. East Foundation. <http://www.eastfoundation.net/our-land/>. Accessed 4 Oct 2015.

Evanno, G., S. Regnaut and J. Gaudet. 2005. Detecting the number of clusters of individuals using the software Structure: a simulation study. Molecular Ecology 14:2611–2620.

Fulbright, T. E., D. D. Diamond, J. Rappole, and J. Norwine. 1990. The coastal sand plain of Southern Texas Rangelands 12:337–340.

Gann, K. 2016. Body and antler size: What's soil got to do with it? Eastfoundation.net. <http://hosted.verticalresponse.com/287068/e7d48d3c9c/1246012115/cc8ceb32c2/>. Accessed 25 April 2016.

Hardy, O. J., and X. Vekemans. 2002. SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. Molecular Ecology Notes 2: 618–620.

Hines, S. 2016. Deer, cattle, and nilgai interactions. Dissertation, Texas A&M University-Kingsville, Kingsville, USA.

Honeycutt, R. L. 2000. Genetic applications for large mammals. Pages 233–259 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice-Hall, Upper Saddle River, New Jersey, USA.

Long, E. S., D. D. Dieffenbach, C. S. Rosenberry, B. D. Wallingford, and M. D. Grund. 2005. Forest cover influences dispersal distance of white-tailed deer. Journal of Mammalogy 86:623– 629.

Manel, S., M. K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: combining landscape ecology with population genetics. Trends Ecology and Evolution 18:189–197.

McCoy, J. E., D. G. Hewitt, and F. C. Bryant. 2005. Dispersal by yearling male white-tailed deer and implications for management. Journal of Wildlife Management 69:366–376.

Miller, B. F., R. W. DeYoung, T. A. Campbell, B. R. Laseter, W. M. Ford, and K. V. Miller. 2010. Fine-scale genetic and social structuring in a central Appalachian white-tailed deer herd. Journal of Mammalogy 91:681–689.

Moran, P. A. 1950. Notes on continuous stochastic phenomena. Biometrika 37:17–23.

Noble, C. W., J. M. Bono, H. K. Pigage, D. W. Hale, and J. C. Pigage. 2016. Fine-scale genetic structure in female mule deer. Western North American Naturalist. 76:417–426.

Nussey, D. H., D. W. Coltman, T. Coulson, L. E. Kruuk, A. Donald, S. J. Morris, T. H. Clutton-Brock, and J. Pemberton. 2005. Rapidly declining fine-scale spatial genetic structure in female red deer. Molecular Ecology 14:3395–3405.

Peakall, R., M. Ruibal, and D. B. Lindenmayer. 2003. Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. Evolution 57:1182-1195.

Porter, W. F., N. E. Matthews, H. B. Underwood, R. W. Sage, and D. F. Behrend. 1991. Social organization in deer: implications for localized management. Environmental Management 15:809–814.

Queller, D. C., and K. F. Goodnight. 1989. Estimating relatedness using genetic markers. Evolution 43:258–275.

Rosenberry, C. S., M. C. Conner, and R. A. Lancia. 2001. Behavior and dispersal of white-tailed deer during the breeding season. Canadian Journal of Zoology 79:171–174.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195-216.

Smith, V. D. and L. S. Campbell. 2017. Texas Parks and Wildlife. Exploring Texas Ecoregions. <https://tpwd.texas.gov/publications/pwdpubs/media/pwd_bk_w7000_0030.pdf> Accessed 20 Feb 2017.

Texas Water Development Board. 2012. Water for Texas 2012 State Water Plan. < http:// www.twdb.texas.gov/publications/state_water_plan/2012/04.pdf>. Accessed 12 Feb 2018.

Texas A&M AgriLife Research and Extension Center. 2015. Annual Report. < http://agrilife .org/lubbock/ files/2016/02/2015-AG-CARES-Report-Website.pdf>. Accessed 12 March 2016.

Texas Parks and Wildlife Department. 2012. Texas Ecoregions. < https:// tpwd.texas.gov/ education/hunter-education/online-course/wildlife-conservation /texas-ecoregions>. Accessed 12 March 2016.

Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370.

Wright, S. 1943. Isolation by distance. Genetics 28:114–138.

CHAPTER II
INFLUENCE OF SPATIOTEMPORAL DROUGHT PATTERNS ON THE CONDITON AND FITNESS OF A FREE-LIVING MAMMAL IN A SEMIARID ENVIRONMENT

INTRODUCTION

Natural populations experience a wide range of temporal and spatial environmental variation. Some of this variation is predictable, such as seasonal changes in the duration of sunlight, temperature, and diet. Other sources of variability are stochastic, and may include inclement weather, nutrition, temperature stress, limited water availability, disease, parasitism, predation, negative social interactions, and injury (Gwazdauskas 1985, Sapolsky 1986, Landys et al. 2006, Sheriff et al. 2012). Environmental variation is especially pronounced in semiarid climates, which cover 30% of the world's land area (Stafford Smith 1996, Sivakumar et al. 2005), and are characterized by high temperatures and high evaporation rates (Huang et al. 2008). High evaporation rates combined with variable precipitation results in low moisture input, frequent droughts, and unpredictable fluctuations in water availability (Fulbright et al. 1990, Thornbrugh 2007, Huang et al. 2008). The frequency, duration, and quantity of precipitation drives plant productivity, and thus food availability for herbivores in semiarid regions (Noy-Mier 1973, Fulbright et al. 1990, Bender and Weisenberger 2005) and herbivore populations are impacted by increasingly unpredictable fluctuations within their environment (Owen-Smith 1990, Kruuk et al. 1999, Ginnett and Young 2000, Ogutu and Owen-Smith 2003, Parker et al. 2009). Yet, less is known about the influence of such environmental variation at the individual level, particularly how drought may influence individual condition and reproduction in semiarid environments.

Animals cope with and respond to both predictable and unpredictable fluctuations within their environment via the hypothalamic-pituitary-adrenal axis (stress axis) and subsequent secretions of stress hormones or glucocorticoids (Wingfield et al. 1998, Boonstra 2013). When stimulated by challenges in the environment, the adrenal gland releases glucocorticoids into the blood stream. Glucocorticoids regulate mobilization of energy and inhibit costly anabolic processes unnecessary for immediate survival, such as growth, digestion, immune function, and reproduction (Sapolsky et al. 2000). Glucocorticoids are intimately tied to an individual's performance and fitness (Breuner et al. 2008, Bonier et al. 2009). Although elevated glucocorticoids may help animals cope with short-term environmental perturbations, chronic exposure to such environmental stressors and subsequent long-term elevations in glucocorticoid hormones may lower body condition and life-time fitness (Sheriff et al. 2012, Dantzer et al. 2014).

White-tailed deer (*Odocolieus virginianus*) living in semiarid environments provide an ideal study organism for examining the link between unpredictable environmental fluctuations and stress physiology, individual condition, and reproduction. White-tailed deer are a common inhabitant of semiarid habitats in North America (Ginnett and Young 2000). In such environments, variability in precipitation influences availability and nutrient content of forage, and is potentially the greatest factor influencing deer population dynamics (DeYoung 2011). For example, in productive environments, up to 29% of fawns conceive their first autumn (DeYoung 2011); however, in highly variable environments fawns rarely breed in their first year, because they cannot reach the minimum body condition required for ovulation (Kie and White 1985, Heffelfinger 2006). Furthermore, in semiarid environments, females rely heavily not only on forage intake, but also endogenous reserves to support reproduction and lactation, their most energetically expensive life history stage (Verme and Ullrey 1984, Cook et al. 2004). Thus, periods of low rainfall (drought) may further constrain females, who already have a high energetic cost for reproduction.

Here, I tested the hypothesis that drought is a main driver of individual condition and fitness in female white-tailed deer living in semiarid environments. To test this hypothesis, I quantified the stress physiology, body condition, and probability of lactation for yearlings (1.5 years old), juvenile (2.5 years old), and mature (≥3.5 years old) deer across 4 study sites in South Texas during 6 years with different drought indexes. Specifically, I predicted that i) in areas and years with greater drought, females would have elevated stress hormone levels reduced body condition, and lower lactation probability; ii) mature females would have reduced stress levels, greater body condition, and increased lactation probability than juveniles, because of energetic trade-offs between growth and reproduction for juveniles; and iii) lactating females would have greater stress levels and reduced body condition than females that were not lactating, because of energetic trade-offs between reproduction and condition (Hewitt 2011).

STUDY AREA

My study was conducted on 4 ranches in the semiarid region of South Texas, USA, which encompass 84,530 ha of native Texas rangeland (Annala 2015). The study sites span a geographic area from the Gulf coast to 145 km inland (Fig. 2.1). These study sites are owned and operated as cattle ranches by the East Foundation. Wildlife is monitored but no explicit management or hunting of native wildlife occurs. All of the sites are surrounded by livestock fences (1.2 m in height), with portions of each ranch boundary

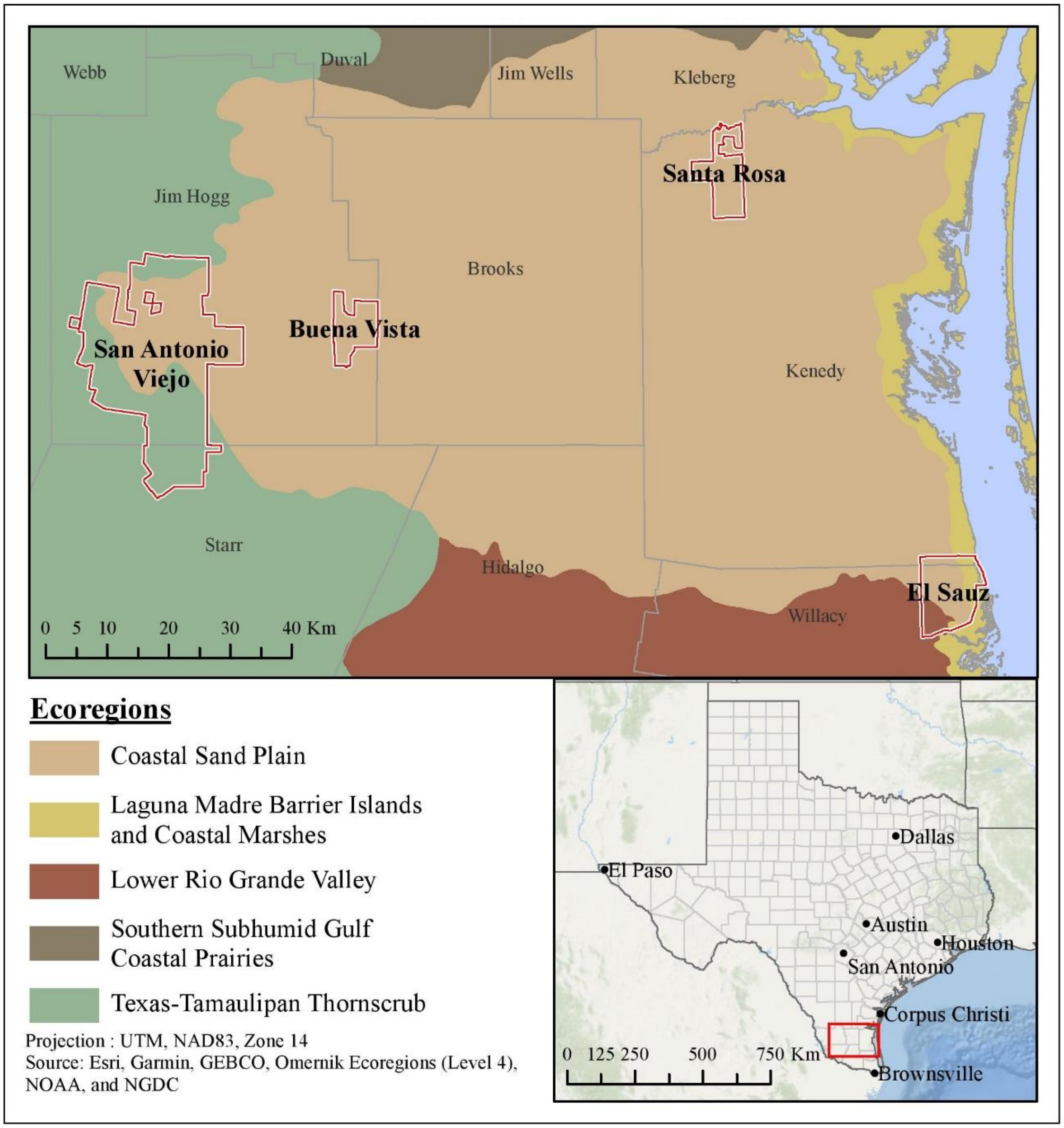

Figure 2.1. East Foundation ranches located across the South Texas Costal Sand Plain and Tamaulipan Thorn Scrub ecoregions.

containing taller fencing (2.5 m). Elevation ranges from 0 to 220 m following an east to west gradient (East Foundation 2016). The 4 sites lie within the Gulf Coastal Plains and South Texas Plains climate divisions. The Gulf Coastal Plains climate division is considered sub-tropical, while the South Texas Plains is sub-tropical humid (Texas Parks and Wildlife Department 2012). Annual average precipitation ranges from 46 to 61 cm and decreases along an east to west gradient (Fulbright et al. 1990, Texas Water Development Board 2012, East Foundation 2016). Variability in daily temperature and precipitation increases inland away from the coast (Texas Parks and Wildlife Department 2012). The region experiences stochastic precipitation, with seasonal peaks in May – June and September – October. Precipitation is often low during November – March and modest in July – August (Fulbright et al. 1990, Smith and Campbell 2017). September receives the highest monthly rainfall with an average of 11.9 cm (Texas A&M AgriLife Research and Extension Center 2015).

In the eastern part of the South Texas region, peak breeding for white-tailed deer is in mid-December, while in the western portion, the peak is during late December (Traweek et al. 1996). Pregnancy rates are high throughout South Texas, and average 95% for adult females (Kie and White 1985, and Traweek et al. 1996). Parturition peaks from July to early August and fawn survival is highly variable and correlated with precipitation (Kie and White 1985, Traweek et al. 1996, Ginnett and Young 2000, Heffelfinger 2006).

The 4 study sites occur in the Coastal Sand Plain and the Tamaulipan Thorn Scrub ecoregions. The Costal Sand Plain consists of grassland savannah interspersed with groves of woody vegetation dominated by live oak (*Quercus virginianus*) and honey mesquite (*Prosopis glandulosa*) groves, sand dunes, and saline habitats (Fulbright et al. 1990). The Tamaulipan Thorn Scrub region consists of thicker thornscrub woodlands with a higher diversity of shrubs and forbs than the Coastal Sand Plain, primarily due to the higher fertility of soils (Hines 2016). The soils are acidic clays, clay loams, and caliche and prone to drought. Prominent species of vegetation are live oak, honey mesquite, brasil (*Condalia hookeri*), prickly pear (*Opuntia spp*), and spiny hackberry (*Celtis pallida*), all interspersed in grassland (Smith and Campbell 2017).

The study sites described below are listed from east (along the coast, wettest) to west (furthest inland, driest). El Sauz is located along the Laguna Madre, near Port Mansfield in Kenedy and Willacy Counties, Texas, USA (lat 26°33’38.1 long -97°29’24.3). The property is in the Coastal Sand Plain ecoregion and consists of 11,201 ha of live-oak woodlands, upland dune topography, open grasslands, and salt marshes (Fulbright et al. 1990, Carr 2015). Precipitation is less variable due to periodic sea-breeze rains from the Gulf of Mexico.

Santa Rosa is 20 km south of Kingsville in Kenedy County, Texas (lat 27°10’33.0 long -97°50’59.3). This 7,471 ha property consists of both Coastal Sand Plain woodland habitat dominated by live oak, and Tamaulipan Thorn Scrub combined with mesquite-huisache (*Acacia* f*arnesiana*) brush communities in heavier soils that developed in an abandoned pasture.

Buena Vista is about 80 km south of Hebbronville in Jim Hogg County, Texas (lat 26°57’17.8 long -98°27’32.8). This 6,110 ha property consists of grassland savannah with widely spaced patches of woody vegetation spaced widely throughout.

San Antonio Viejo is about 60 km southwest of Hebbronville in Jim Hogg and Starr Counties, Texas (lat 26°54’20.5 long -98°36’34.7). This 57,011 ha property lies partially in the Coastal Sand Plain and the Tamaulipan Thorn Scrub ecoregions (Annala 2015). Most of the ranch is composed of Tamaulipan Thorn Scrub and grassland, but the eastern section is within the Coastal Sand Plain ecoregion, where the vegetation community consists of mesquite savannah with small patches of live oak groves.

METHODS

Deer Capture

White-tailed deer were captured at random using a net gun deployed from a helicopter (Krausman et al. 1985) during 4 consecutive weekends in October – November during 2011 – 2016. Captured animals were restrained and hobbled, fitted with a blindfold, and transported by vehicle to a central processing station at each site. At the processing station, individuals were aged according to tooth replacement and wear criteria (Severinghaus 1949) and placed into age classes ranging from fawn to ≥6.5 years old. I sexed individuals and marked them with numbered steel ear tags (National Band and Tag Company, New Port, KY), replacing missing or damaged tags as necessary. I assigned a body condition score ranging from 1 – 5, depending on fat deposition on neck, hips, spine, and rump (Jefferies 1961, Edmondson et al. 1989). Scores of 1 indicated animals with depleted subcutaneous fat deposits, prominent pelvis and spine, and extensive muscle atrophy; whereas a score of 5 indicated an individual with well-developed fat reserves that obscured the pelvis, spine and ribs. Lactation status was determined by the presence of swollen teats.

To estimate glucocorticoids of white-tailed deer, I collected 2-30 fecal pellets directly from each deer's rectum in 2015 and 2016. Fecal glucocorticoid metabolites (FGM; plasma glucocorticoids are metabolized and excreted via the feces) reflect plasma glucocorticoids over a set period of time (Sheriff et al. 2010), 10-14 hrs for white-tailed deer (Millspaugh et al. 2004). Therefore, FGM levels may provide an accurate assessment of stress without the bias of capture-induced increases in glucocorticoids and may provide a more accurate assessment of long-term cortisol levels (Sheriff et al. 2011; Dantzer et al. 2014). Immediately upon collection, fecal samples were placed on wet ice for up to 24 hrs before transport to the laboratory, where they were stored at -20°C until assayed. Individuals were then released on site.

Fecal Glucocorticoid Metabolite Assay

Fecal glucocorticoid metabolite levels were assayed using a standard I^{125} double-antibody radioimmunoassay (RIA) kit (MP Biomedicals, Solon, OH) to measure corticosterone metabolites that has been validated for specific use in white-tailed deer (Millspaugh et al. 2004). I followed the manufacturer's instructions for the RIA assay, but halved all reagents (Wasser et al. 2000, Millspaugh et al. 2004). Briefly, I freeze-dried samples using a lyophilizer for 24 hrs and finely ground and mixed using a mortar and pestle. I extracted cortisol metabolites by adding 2 mL of 90% methanol to 0.20 g of dried feces and vortexing for 30 min at 1,500 rpm. I centrifuged samples at 1900 *g* for 20 min, removed the supernatant, diluted (1:100) with assay buffer, and stored the samples at -20°C until assayed with the RIA kit. The average inter- and intra-assay coefficient of variation (CV) were 2.86% and 1.7%, respectively. Any samples with a CV >25% were re-analyzed.

Statistical Analysis

Age Classes.— For females captured in 2011 – 2016, age estimates were adjusted for recaptured deer that were first captured as fawns or 1.5 years, as they were considered known ages, while age was estimated for individuals captured ≥2.5 years old via tooth replacement and wear criteria. I classified adult females into 3 age classes: yearling (1.5 years old), juvenile (2.5 years old) and mature (≥3.5 years old). Since only 4 lactating yearlings were recorded, they were excluded from the lactation analysis.

*Drought Index.—*To quantify the effects of drought, I retrieved the monthly Palmer Modified Drought Indices (PMDI) data for Texas Climate Region 11 from NOAA (Heddinghaus and Sabol 1991). This drought index uses temperature and precipitation data to estimate moisture supply and demand within a two-layer soil model for a dictated period of time (Heddinghaus and Sabol 1991). I averaged the monthly PMDI values from March – July (spring) to represent conditions that may influence lactation rates (Kie and White 1985), and from September – November (autumn) to model conditions that may influence female body condition prior to capture. Monthly PMDI values range from -10 to 10, where negative values represent drought conditions.

Female Condition and Fitness.— Stress physiology. I compared mean FGMs across 3 age classes and between spring PMDI values for 2015 and 2016 for all females. I used a linear model to test the effects of spring PMDI, lactation status, and site, including their interactions, on FGMs for mature females on El Sauz and San Antonio Viejo captured in 2015 and 2016; the data set was restricted to mature females and 2 sites because of sample size limitations. Variances among levels of PMDI, lactation status, and site were heterogeneous (Levene's test; Levene 1960 and residuals were non-normally distributed

(Shapiro-Wilk test; Shapiro and Wilk 1965) for some combinations of these factors; therefore, I analyzed log-transformed data. The 4 factors were set as fixed variables and the model included all interactions. I used the GLM procedure in SAS 9.4 (SAS Institute, Inc., Cary, NC).

Body condition. I compared the distribution functions of body condition scores among sites for combinations of age class, lactation status, and study site using the Kruskal-Wallis test for females captured in 2011 – 2016. If the distributions were different, I tested difference in means using an F-test. I used a linear model using the GLM procedure to determine partial R^2 (Nakagawa and Schielzeth 2012) for effects of autumn PMDI and site on body condition score for each female age class and lactation status.

Lactation. To evaluate the relationship between probability of lactation for year-specific spring PMDI and juvenile and mature females across the 4 sites, I analyzed the relationship between these factors with a generalized linear model. Spring PMDI, female age class, site, and their interactions were fixed effects. I tested the hypotheses that probability of lactation was not affected by spring PMDI, age class or their interaction with the GLIMMIX procedure in SAS using a logit link function.

RESULTS

Drought Index

Mean spring PMDI values from 2011 – 2016 ranged from -5.60 in 2013 to 7.69 in 2015 (Table 2.1). The Texas Climate Region 11 experienced drought conditions during spring 2011 – 2013 (average PMDI = -4.40). Mean spring PMDI for 2011 – 2016 was -3.72. The Climate Region 11 also experienced drought during autumn, 2011 and 2012, while

Table 2.1. Mean March – July (spring) and August – November (autumn) monthly Palmer Modified Drought Indices according to National Oceanic and Atmospheric Administration for 2011 – 2016 in Region 11 in South Texas, USA. Indices generally range from -10 – 10 and negative values indicate drought conditions.

Year	**Spring PMDI**	**Autumn PMDI**
2011	-4.17	-1.91
2012	-3.42	-5.19
2013	-5.60	1.09
2014	0.45	1.27
2015	7.69	0.56
2016	0.96	0.34

the rest of the years were barely above drought conditions. Mean autumn PMDI values from 2011 – 2016 ranged from -5.19 in 2012 to 1.27 in 2014.

I captured 1,878 individual female white-tailed deer, of which 452 were lactating and 1,426 were not (Table 2.1, Appendix A.). I captured 187 yearlings, 182 juveniles, and 1,509 mature females. Twenty-one percent of juvenile and mature females had first been captured as fawns or at 1.5 years old and therefore were of known age.

Female Condition and Fitness.

Stress Physiology.— Fecal glucocorticoid metabolites for all females were highly variable and ranged from 14.5 - 462.4 ng/mL (Fig. 2.2). Mature females had the greatest range of FGMs (Appendix B, Table 2.1) Means FGMs among age classes were not different ($F_{1,126}$ = 1.79, P = 0.17). Mean FGMs between spring PMDIs were not different ($F_{1,127}$ = 0.29, P = 0.59; Fig 2.3). Mature female mean FGMs were not influenced by spring PMDI ($F_{1,71}$ = 1.64, P = 0.20), site ($F_{1,71}$= 0.30, P = 0.59; Fig 2.4) or lactation status ($F_{1,71}$ = 0.02, P = 0.89). I found a weak interaction between lactations status and spring PMDI ($F_{1,71}$= 2.91, P = 0.09), but none of the simple effect tests embedded in this interaction were significant ($F_{1,71}$, $P \geq 0.17$).

Body Condition.— The empirical distribution functions of body condition scores differed between non-lactating and lactating females (KSa = 8.15, $P < 0.01$; Fig. 2.5); generally, quantiles for non-lactating animals were higher than corresponding quantiles for lactating animals. Mean body condition score was higher for non-lactating females ($\bar{X}$ = 3.38 ± 0.02) than that of lactating females ($\bar{X}$ = 2.51 ± 0.03; $F_{1,800.4}$ = 467.88, $P < 0.01$). The empirical distribution functions of body condition scores also differed between age classes, where mature females generally had higher quantiles of body condition

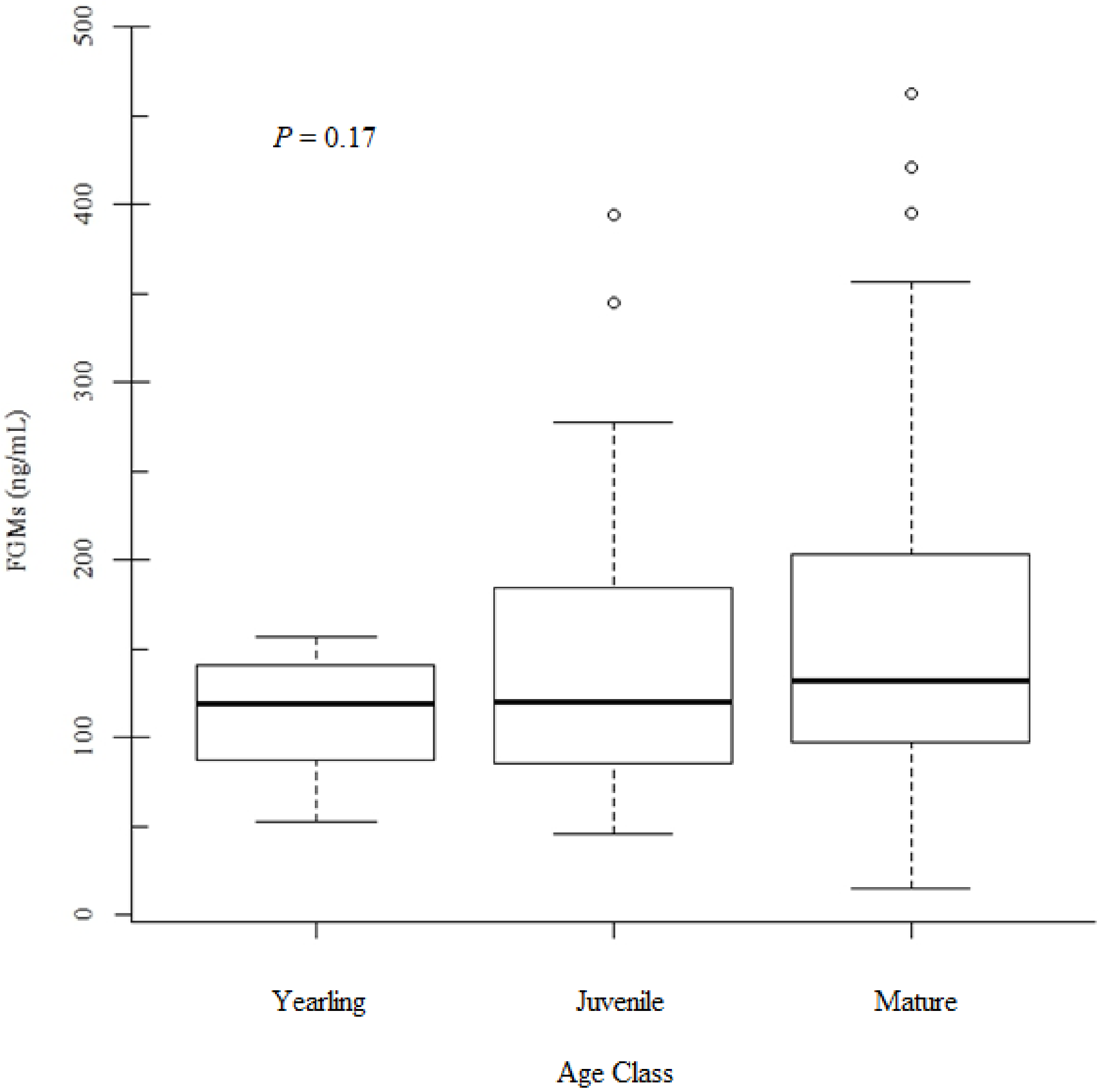

Figure 2.2. Fecal glucocorticoid metabolites (FGMs) for yearlings (1.5 years old), juvenile (2.5 years old), and mature (≥3.5 years old) female white-tailed deer. Females were captured in 4 study sites in South Texas, USA. Captures occurred in October – November 2015 – 2016.

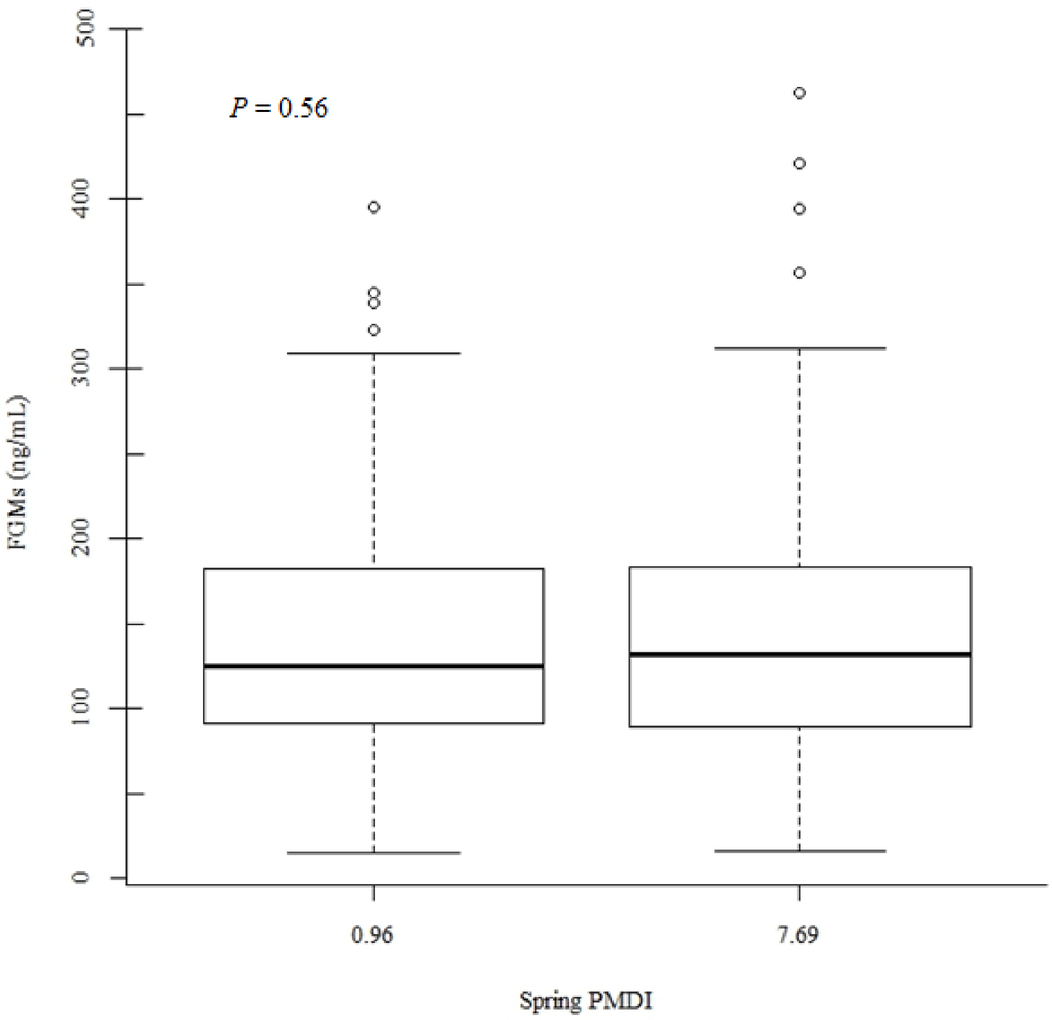

Figure 2.3. Fecal glucocorticoid metabolites (FGMs) for female (≥2.5 years old) white-tailed deer. Females were captured on 4 study sites in South Texas, USA. Captures occurred during October – November during 2015 (PMDI = 7.69) and 2016 (PMDI = 0.96). Monthly Palmer Modified Drought Indices (PMDI) were averaged over March – July from National Oceanic and Ocean's Administration for Region 11 for Texas.

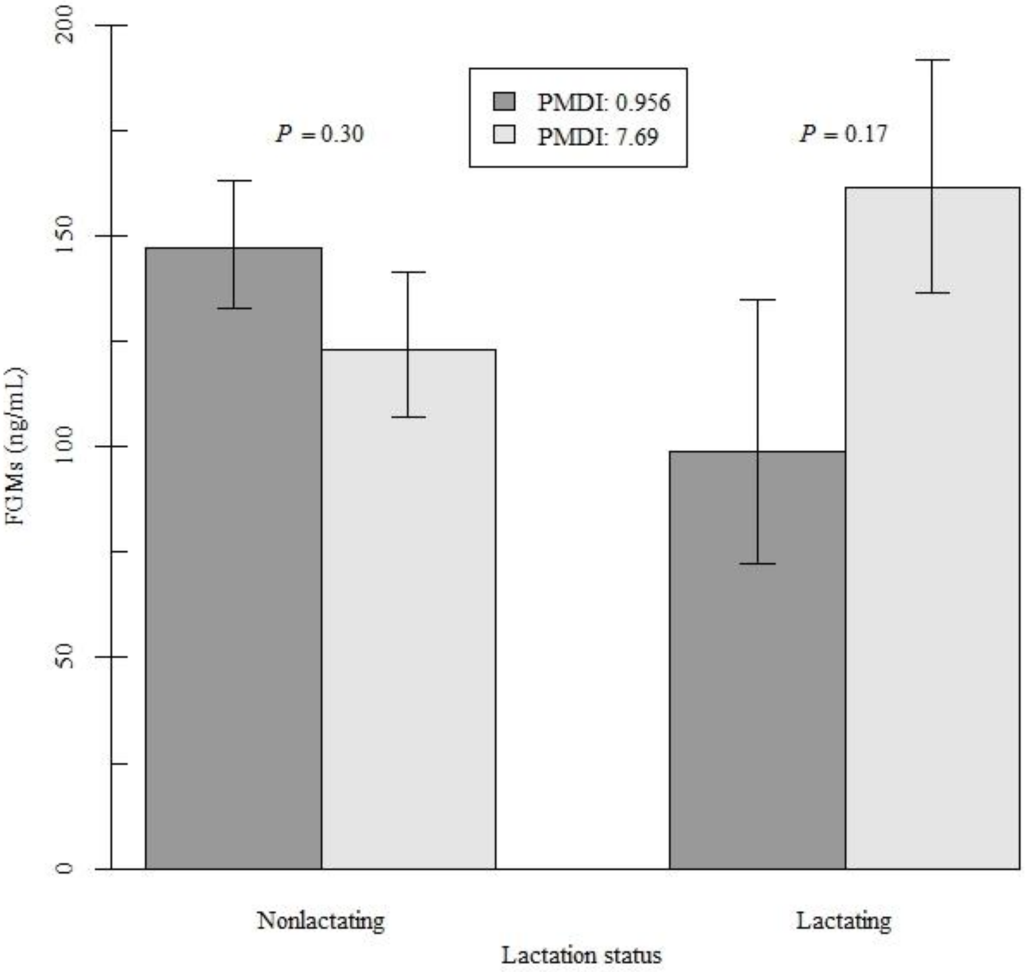

Figure 2.4. Difference between mean fecal glucocorticoid metabolites (FGMs) of mature (≥ 3.5 years old) female white-tailed deer for the effects of lactation status, March – July (spring) Palmer Modified Index Indices (PMDI), and study site. Females were captured on 2 study sites located in South Texas; El Sauz and San Antonio Viejo, representing the most eastern and western site, respectively. Captures occurred during October – November 2015 – 2016. Variables were set as fixed in the model. Analysis was done on log-transformed FGM data, but presented in back-transformed means.

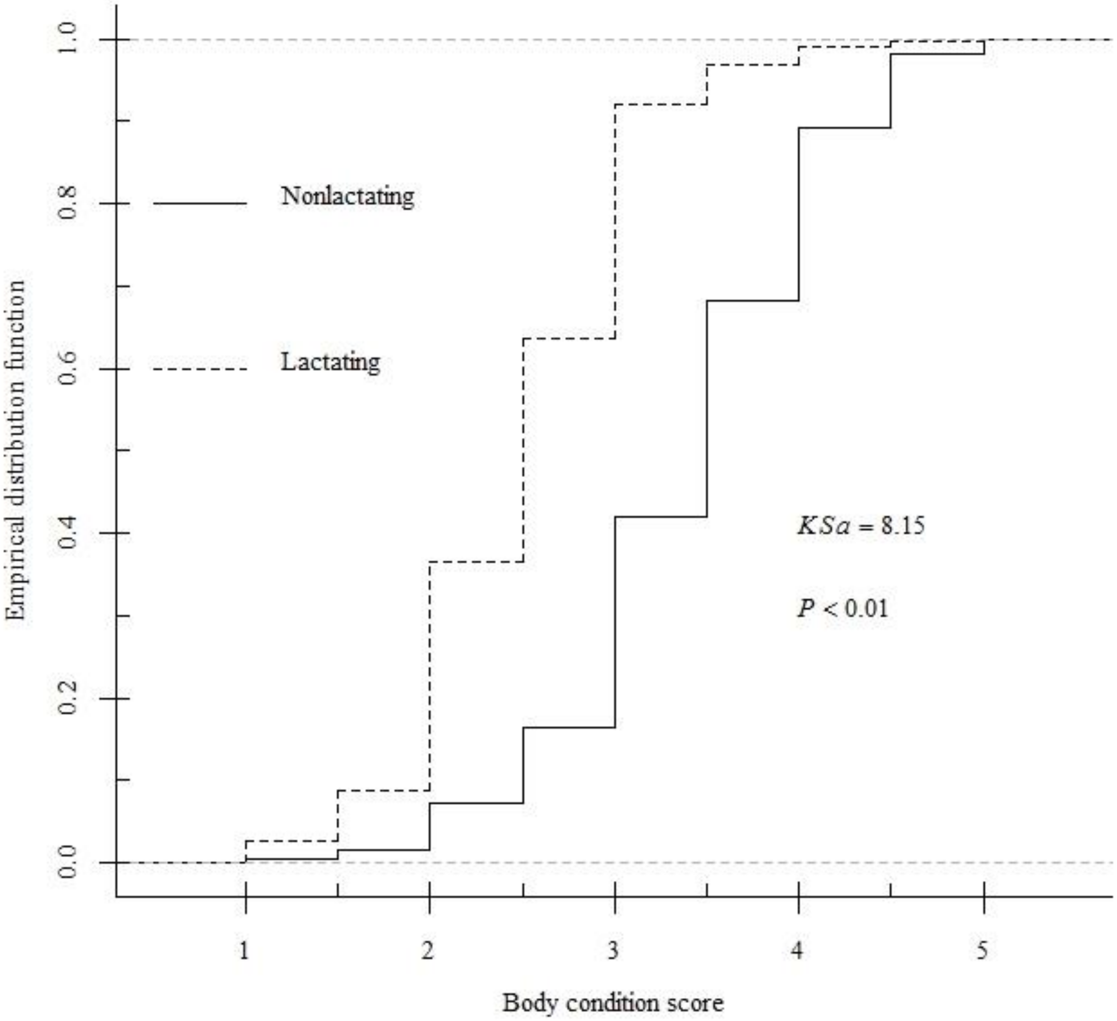

Figure 2.5. Empirical distribution functions of body condition scores for lactating and nonlactating female white-tailed deer (≥2.5 years old). Females were captured on 4 study sites in South Texas, USA. Captures occurred during October – November 2011 – 2016. Body condition scores range from poor to excellent, where 1 represents severely depleted subcutaneous fat and extensive muscle atrophy, and 5 represents well-developed fat reserves.

score than juveniles (KSa = 1.90, P = < 0.01; Fig. 2.6). Mean body condition score was higher for non-lactating mature females ($\bar{X}$ = 3.40 ± 0.03) than for non-lactating juvenile females ($\bar{X}$ = 3.23 ± 0.05; $F_{1,265.4}$ = 9.62, P < 0.01). The empirical distribution functions of body condition scores did not differ between lactating juvenile ($\bar{X}$ = 2.64 ± 0.17) and mature females ($\bar{X}$ =2.50 ± 0.03, KSa = 0.30, P = 0.99; Fig. 2.7).

The influence of site on the distribution of body condition scores for age class and lactation status varied among age groups (Fig. 2.8; Table 2.3). Site influenced the distribution of body condition scores for non-lactating juvenile females (χ^2_3 = 23.61, P = 0.01), lactating juvenile females (χ^2_3 = 8.60, P = 0.04), and lactating mature females (χ^2_3 = 20.60, P = 0.01). Site had a weaker effect on the distribution of body condition scores for non-lactating mature females (χ^2_3 = 6.51, P = 0.09). Generally, Santa Rosa and higher mean body condition scores.

In separate analyses for each age class and lactation status, site and autumn PMDI did not consistently explain similar variation in female body condition score (Table 2.4). For example, the partial R^2 for the site effect explained little variation (R^2 = 1%) for non-lactating mature females, but 32% of the variation in body condition score for lactating juvenile females. Meanwhile, autumn PMDI had a weak influence on body condition score for all combinations of age class and lactation status.

Lactation Status. —Three per cent of yearlings, 11% of juveniles, and 28% of mature females were lactating in 2015 – 2016. Female age class and spring PMDI interacted ($F_{1,1397}$ = 4.10, P < 0.04; Fig 2.9) in their effects on probability of lactation. Female age class significantly influenced probability of lactation. Specifically, the odds of lactation

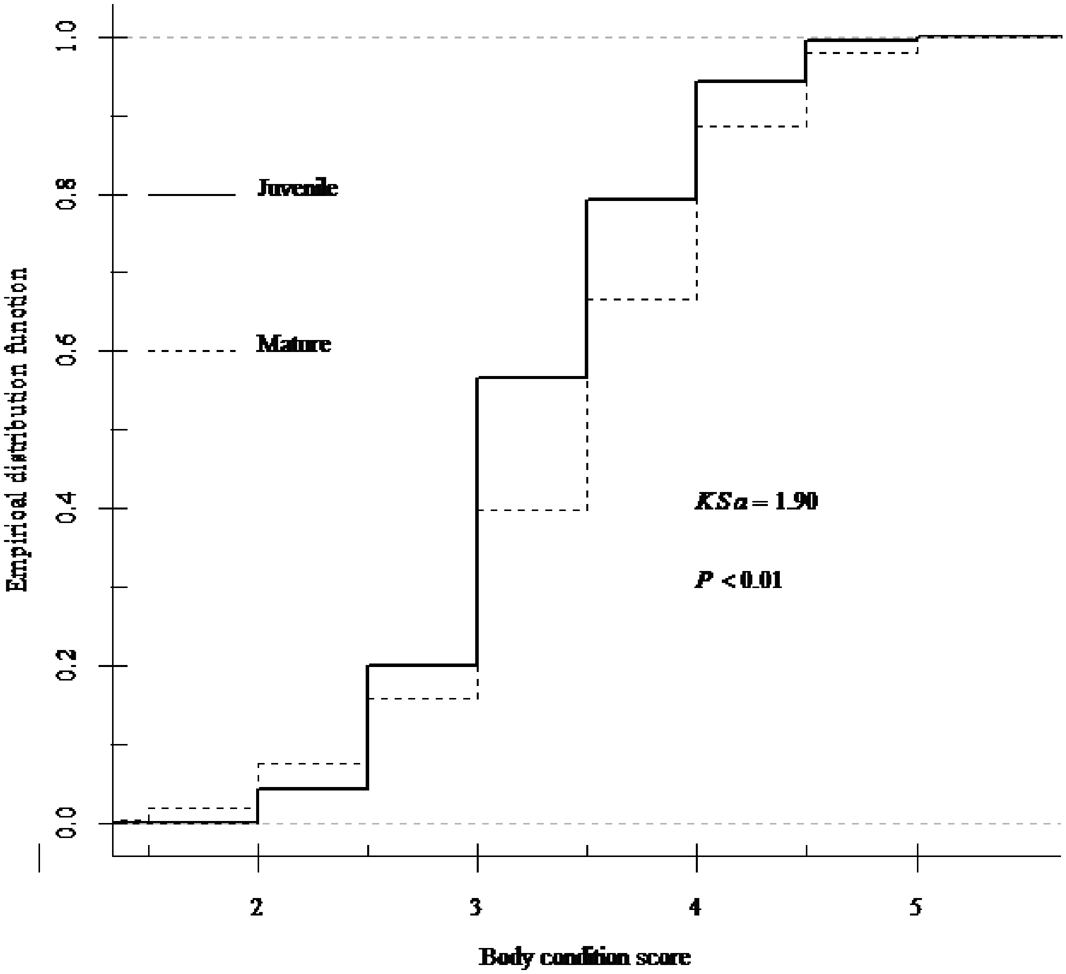

Figure 2.6. Empirical distribution functions of body condition scores for nonlactating juvenile (2.5 years old) and mature (≥3.5 years old) female white-tailed deer. Females were captured on 4 study sites in South Texas, USA. Captures occurred during October – November 2011 – 2016. Body condition scores range from poor to excellent, where 1 represents severely depleted subcutaneous fat and extensive muscle atrophy, and 5 represents well-developed fat reserves.

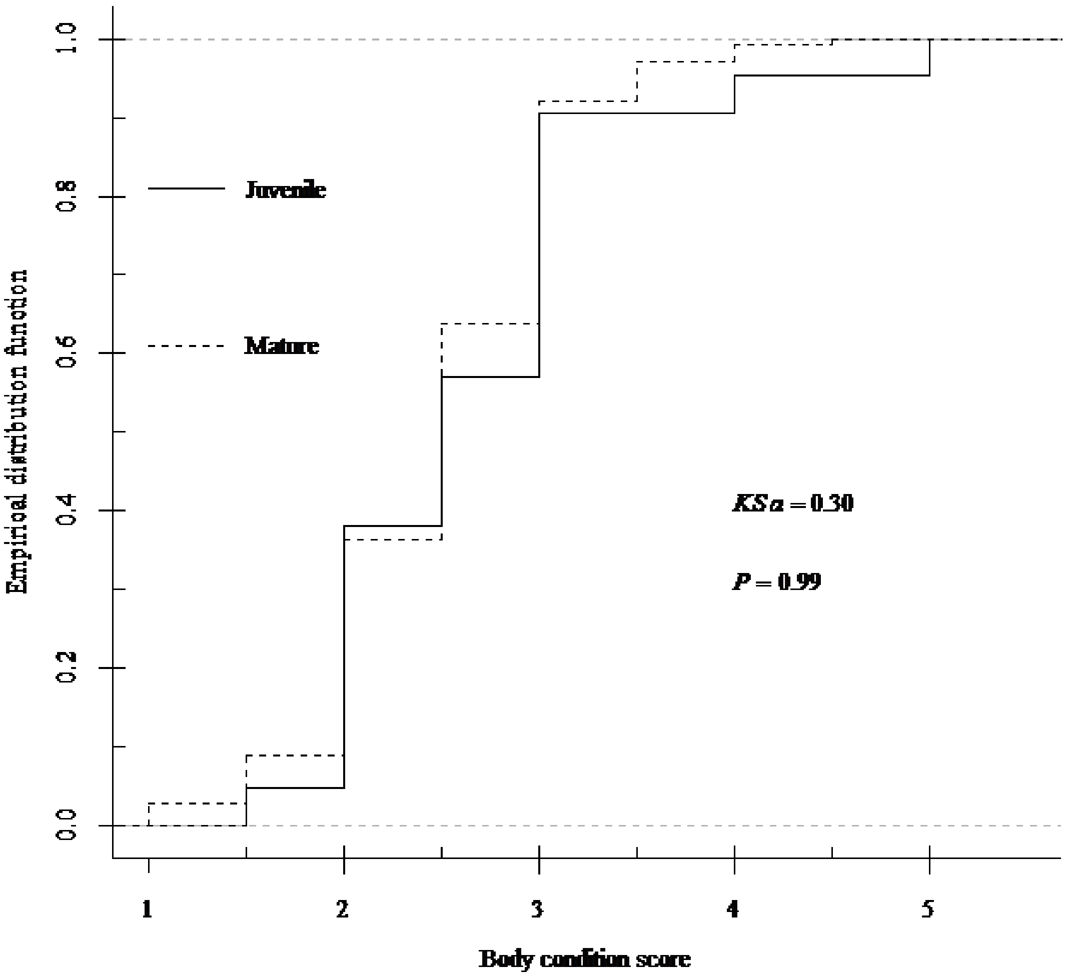

Figure 2.7. Empirical distribution functions of body condition scores for lactating juvenile (2.5 years old) and mature (≥3.5 years old) female white-tailed deer. Females were captured on 4 study sites in South Texas, USA. Captures occurred during October – November 2011 – 2016. Body condition scores range from poor to excellent, where 1 represents severely depleted subcutaneous fat and extensive muscle atrophy, and 5 represents well-developed fat reserves.

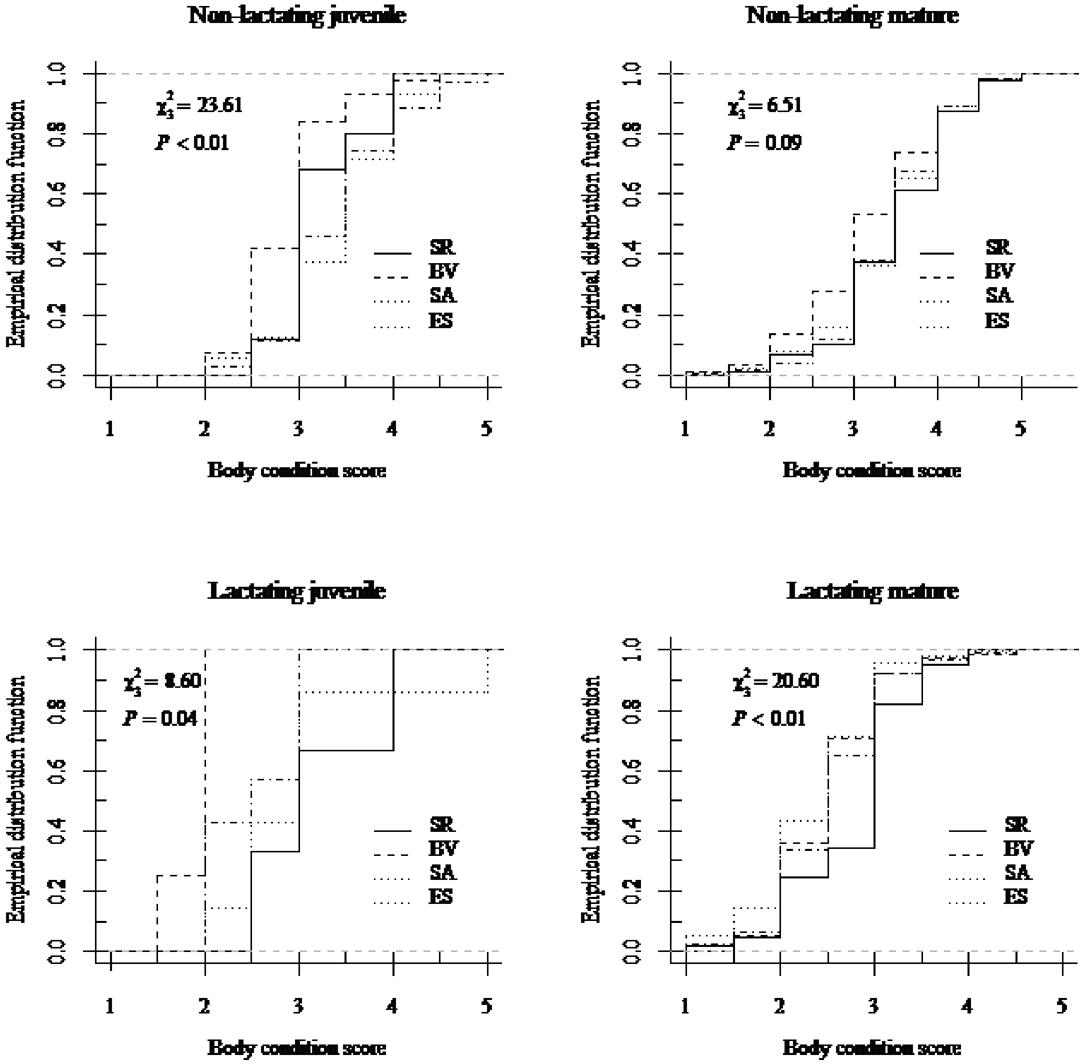

Figure 2.8. Distribution functions of body condition scores among 4 study sites for combinations of lactating and nonlactating juvenile (2.5 years old) and mature (≥3.5 years old) female white-tailed deer. Females were captured on 4 study sites in South Texas, USA. Captures occurred during October – November 2011 – 2016. Body condition scores range from poor to excellent, where 1 represents severely depleted subcutaneous fat and extensive muscle atrophy, and 5 represents well-developed fat reserves.

Table 2.2. Female white-tailed deer body condition scores among 4 study sites for juvenile (2.5 years old) and mature (≥3.5 years old) females by lactation status (NL = Nonlactating; L = lactating) for selected quantiles. Females were captured 2011 – 2016 in 4 study sites located in South Texas, USA. Females were captured on 4 study sites in South Texas, USA. Captures occurred during October – November 2011 – 2016. Body condition scores range from poor to excellent, where 1 represents severely depleted subcutaneous fat and extensive muscle atrophy, and 5 represents well-developed fat reserves.

				Selected Quantiles		
Lactation status	Age class	Site	*	Quantile 0.25	Quantile 0.50	Quantile 0.75
NL	Juvenile	El Sauz	a	3.0	3.5	4.0
		Santa Rosa	a	2.5	3.0	3.0
		Buena Vista	b	2.0	2.5	3.0
		San Antonio Viejo	a	2.5	3.0	3.0
	Mature	El Sauz	a	3.0	3.5	4.0
		Santa Rosa	a	3.0	3.5	4.0
		Buena Vista	a	3.5	3.5	4.0
		San Antonio Viejo	a	3.0	3.5	4.0
L	Juvenile	El Sauz	a	2.0	2.5	3.0
		Santa Rosa	a	2.5	3.0	4.0
		Buena Vista	b	1.75	2.0	2.0
		San Antonio Viejo	a	2.5	3.0	3.0
	Mature	El Sauz	b	2.0	2.5	3.0
		Santa Rosa	a	2.5	3.0	3.0
		Buena Vista	bc	2.0	2.5	3.0
		San Antonio Viejo	c	2.0	3.0	3.0

*****Sites for a lactation status and lactation status followed by the same lower-case letter do not differ ($P < 0.05$) with respect to distribution functions.

Table 2.3. Partial R^2 values for effects of study site and September – November (autumn) monthly Palmer Modified Drought Indices (PMDI) on body condition scores for juvenile (2.5 years old) and mature (≥3.5 years old) female white-tailed deer by lactation status. Females were captured on 4 study sites in South Texas, USA. Captures occurred during October – November 2011 – 2016.

Lactation status	Age class	Site effect	Autumn PMDI effect
Nonlactating	Juvenile	0.10	0.01
	Mature	0.01	0.04
Lactating	Juvenile	0.32	0.06
	Mature	0.05	0.00

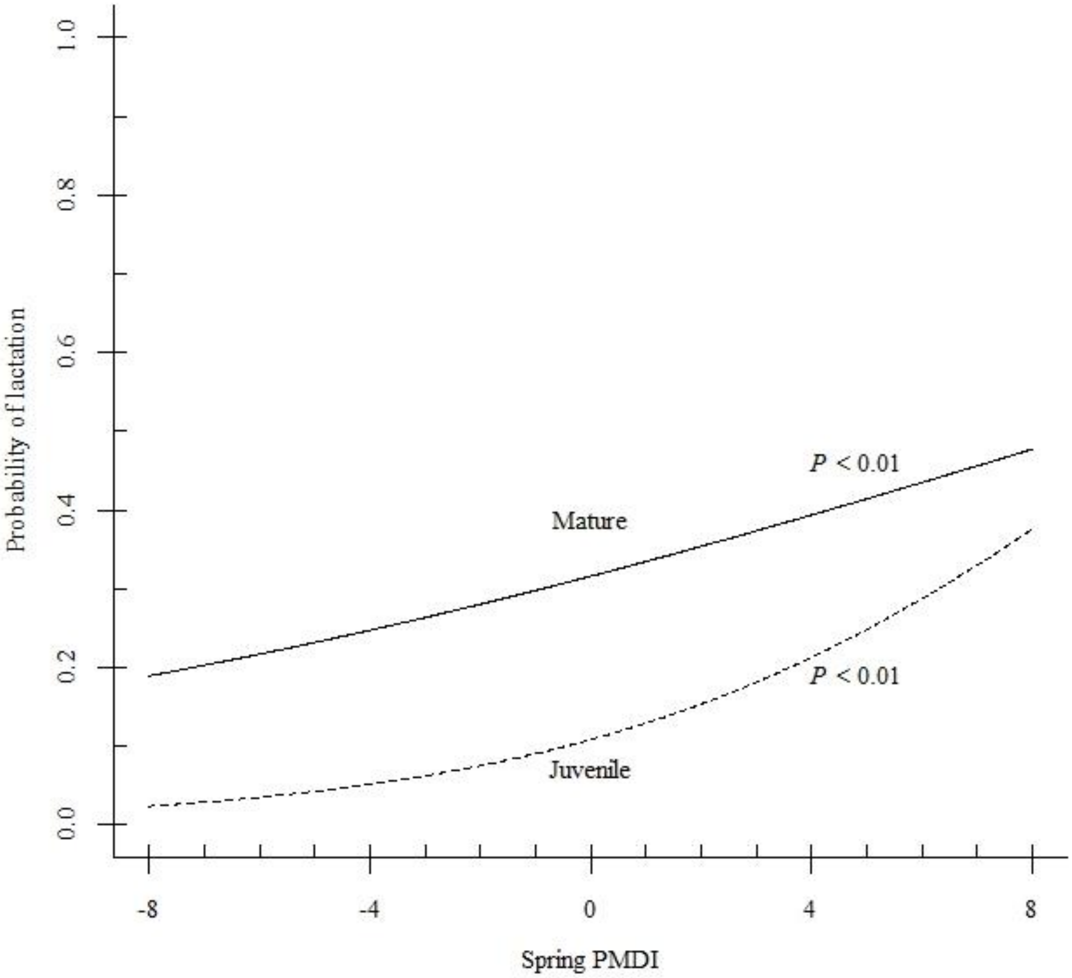

Figure 2.9. Probability of lactation for juvenile (2.5 years old) and mature (≥3.5 years old) white-tailed deer females and March – July (spring) monthly Palmer Modified Drought Indices (PMDI). Females were captured on 4 study sites located in South Texas, USA. Captures occurred during October – November 2011 – 2016.

increased by 22% for each unit increase in spring PMDI for juvenile females and 9% for mature females. For example, under the wettest conditions (spring PMDI = 7.69 in 2015), mean probabilities of lactation for mature deer (0.47 ±0.05) and juveniles (0.40 ± 0.10) did not differ ($t_{1397} = -0.98$, $P = 0.11$, Table 2.4). However, under the driest conditions (spring PMDI = -5.6), probability of lactation for mature deer (0.22 ± 0.02) was higher ($t_{1397} = -4.02$, $P = 0.05$) than probability of lactation for juveniles (0.04 ± 0.02).

DISCUSSION

In the semiarid region of South Texas, lactation patterns of white-tailed deer were strongly related to spring drought conditions. Mature females had a greater probability of lactation compared to juvenile females, and spring drought conditions had less influence on lactation probability of mature females compared to juveniles. Spring PMDI (drought index) did not influence FGMs and autumn PMDI influenced the body condition of females weakly. However, site had a modest effect on body condition, with Santa Rosa overall having higher mean body condition scores than the other sites. As expected, non-lactating mature females had greater body condition than non-lactating juveniles, and surprisingly, all lactating females had similar body condition (regardless of age class).

Stress

Contrary to my predictions, I found that neither spring drought conditions nor site influenced autumn FGM levels in females. Although long-term exposure to environmental stressors, such as drought, has been linked to elevated FGMs in free-living, seasonally breeding animals (Wingfield 1994, Cavigelli 1999, Lynch et al. 2002, Romero et al. 1997, Boonstra 2004, Reeder and Kramer 2005), it is likely that in my study, the stressors experienced during March – July did not carry over to influence the

Table 2.4. Mean probability of lactation (SE) for juvenile (2.5 years old) and mature (≥3.5 years old) white-tailed deer females coinciding with the driest, wettest, and average March – July (spring) monthly Palmer Modified Drought Indices (PMDI) from 2011 – 2016. Females were captured on 4 study sites located in South Texas, USA. Captures occurred during October – November 2011 – 2016.

			Age class	
Moisture conditions	Year	Spring PMDI	Juvenile	Mature
Driest	2013	-5.60	0.04 (0.018)	0.22 (0.017)
Wettest	2015	7.69	0.36 (0.097)	0.47 (0.047)

stress physiology of white-tailed deer in October – November. It would be important to investigate how autumn PMDI levels may influence stress levels in October and November.

I also found that FGM levels were similar between all age classes. I predicted that fawns and juveniles would have greater FGM levels because of their increased maintenance costs due to growth, their increase susceptibility to predation, and their lower rank in the dominance hierarchy (Sapolsky 1986, Gesquirere et al 2008, Jachowski et al. 2015). For example, Jachowski et al. (2015) found that on average, juvenile white-tailed deer had slightly higher FGMs compared to adults in a captive environment. My results suggest that deer FGMs reflect the environment they are experiencing, which was similar across all deer in both years. Although young deer may pay higher costs for growth and experience greater predation risk, adults may invest more in reproduction. Previous studies have provided conflicting support for the influence of age and reproductive status on stress. For instance, breeding female red squirrels (*Tamiasciurus hudsonicus*) had greater FGMs than non-breeding females (Dantzer et al. 2014), while reproductive stage had no influence on FGMs in captive red deer (*Cervus elaphus*; Huber et al. 2003). Further, although I expected juveniles to have greater FGMs because of their lower dominance ranking, dominant individuals may have higher FGMs compared to subordinates (Gesquirere et al 2008). Clearly, more work is needed to understand the drivers of stress physiology in free-living white-tailed deer.

Body Condition

I found that female body condition was influenced by spring PMDI, age class, and lactation. Body condition score for nonlactating mature females was consistent among capture location, likely because mature females who were not lactating have the lowest nutrient requirements and were therefore less responsive to different conditions among sites. In contrast, body condition scores of all juvenile females and lactating mature deer were influenced by study site, where females at Santa Rosa generally had greater body condition scores. These classes of deer had elevated nutritional requirements and therefore were responsive to differences among study sites. Lactating juvenile females were the most susceptible to changes in available resources because they have the largest energetic costs. Further investigation must be done to determine why Santa Rosa had greater body condition scores. I predicted that autumn body condition may largely depend on summer – autumn nutrition and thus PMDI values from September – November would explain some variation in autumn female body condition (Tollefson et al. 2010). Variation in autumn moisture explained the most variation in body condition scores for lactating juvenile females. However, autumn drought conditions explained only 13% variation in autumn body condition scores for nonlactating mature females. This evidence, in addition to the sensitivity of lactating juvenile females to spring PMDI and study site, supports the trend that nonlactating mature females are not as sensitive to nutritional conditions.

When not lactating, mature deer have better body conditions than juvenile deer. This implies that adult deer have more excess energy and nutrients. The excess energy and nutrients could be allocated to reproduction and would enable mature females to be more successful in raising fawns. However, when lactation is a factor, body condition scores for mature and juvenile females did not differ. Since body condition of females is the integrator of nutritional demands and available nutrition (Parker et al. 2009), this analysis demonstrates that juvenile females, that are still allocating energy towards growth, cannot build as large of endogenous reserves as females that are done growing when living in the same forage conditions. My prediction that body condition scores were lower for lactating females was met, since fat deposition and mobilization change as physiological requirements change (Parker et al. 2009). However, body condition scores were not different between age classes for lactating females like I predicted. The fact that body condition scores diminished to an equal extent for both age classes support the intense energetic cost associated with lactation (Hickling et al. 1991), as peak lactation may be 6.7 times basal metabolic rate (National Research Council 2007) and suggests a threshold in body condition beyond which a female may be reluctant (from a nutritional standpoint) to push herself when using reserves to support lactation.

Lactation Status

I found that lactation rates were low overall, indicating limiting factors in this semiarid region. For example, across the range of white-tailed deer nearly 100% of juveniles and adults breed, and fawns can be bred if they meet the minimum body condition for ovulation (Kie and White 1985, Heffelfinger 2006). Lactation rates <30% indicate that most females lose their fawns each year. I suspect that the low levels of lactation may be indicative of density-independent factors such as stochastic variation in environmental conditions and limited nutrition overall (Ginnett and Young 2000). Environmental variability plays an important role for ungulates across the world, for example, bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*), and kudu (*Tragelaphus imberbis*) populations are limited by precipitation (Bender and Weisenberger 2005). I show environmental variability and particularly drought conditions may play significant roles limiting autumn lactation and successful weaning of offspring. Given the overall reduction in lactation rates, and in particular for juvenile females, drought conditions in spring may have a large influence on population dynamics for deer in semiarid environments. Appreciating these effects may have significant management implications associated with recruitment pulses that may be predicted dependent upon previous spring conditions.

I found that spring drought conditions significantly reduced autumn probability of lactation in white-tailed deer. Interestingly, mature females were more resistant to the effects of drought than juvenile females; in the driest year 22% of mature females were lactating compared to 34% in the wettest year, however, only 4% of juveniles were lactating in the driest year compared to 22% in the wettest year. Spring moisture conditions likely drive food availability both in spring but also throughout summer, and this is a critical and energetically expensive time for females that are lactating. Given that juveniles are still growing and costs to growth, it is not surprising that they are also more susceptible to spring drought conditions compared to mature females that have reduced maintenance costs and can put more energy towards lactation.

MANAGEMENT IMPLICATIONS

Understanding mechanisms that may limit or regulate wild herbivore populations is crucial for effective management (Ginnett and Young 2000, Bender and Weisenberger 2005). Relationships between variable environmental conditions and female physiology and reproduction also have important implications for the sustainable management of harvested populations (Ginnett and Young 2000). South Texas is virtually all private land, much of which is leased for hunting. Management practices for deer populations are usually based on the assumption of density-dependent population responses (DeYoung 2011). However, I have demonstrated that the environment may play an important role causing deer populations in semi-arid environment to function more as density-independent populations. Thus, the traditional concept of carrying capacity for large herbivore in semiarid environment needs revision to manage white-tailed deer when their populations function under a density-independent paradigm (Bender and Weisenberger 2005).

The implications of nutrition to management and conservation are often not realized (Parker et al. 2009). If it is a drought season, females are not only expending additional energy to search for food, but the food available may be lower in quality. In addition, drought conditions usually coincide with warmer than average temperatures. Providing thermal cover for animals to lower thermoregulatory expenditures may help wildlife with their energetic requirements (Parker et al. 2009) potentially increasing the potential for greater endogenous reserves.

Semiarid regions are prone to periods of drought, and as I have demonstrated, drought conditions may be related to reproduction and recruitment patterns and potentially the reproductive capability of white-tailed deer populations. As climate change proceeds, variation in the frequency and intensity of precipitation are expected to increase, shifting the ranges of arid environments in the southwestern United States, and across the globe (Ragab and Prudhomme 2002). This intensifying climactic variation and shifts in climactic conditions associated with climate change have major implications for populations of many ungulate species. Specifically, increases in global temperature are expected along with changes in precipitation distribution, frequency, and duration, and patterns of evapotranspiration, runoff and soil moisture (Ragab and Prudhomme 2002). Vegetation growth rates and the changes in soil moisture regime will also be affected (Ragab and Prudhomme 2002). Potential involvement of climactic influence has not been explored for many species population declines throughout Africa (Ogutu and Owen-Smith 2003). Climatic shifts and extreme climatic variability could actually underlie local population extirpations currently occurring in Africa (Ogutu and Owen-Smith 2003).

In addition to nutrition, the age structure of a population is critical to population success. Age structure of females may augment limitations of reproduction caused by drought, or other environmental availability. My study emphasized the importance of mature females for successful reproduction. If mature females are not managed for properly in semiarid environments where fawn recruitment is already low and erratic, the population may decline. When the environment is conducive to high recruitment, it is crucial to maintain a population of reproductive females. My evidence of the effects of lactation and body condition of females demonstrates the importance of understanding why body condition may be low for particular females. Low body condition in autumn may be indicative of the reproductive capabilities of that female.

Lastly, measures of glucocorticoid levels can provide quantitative information about how environmental changes impacts individuals. Monitoring these hormone levels may act as an early warning system to inform future population declines (Sheriff et al. 2011). Fecal hormone levels represents a good indicator of population or individual health, and feces can be easily collected from the environment.

LITERATURE CITED

Annala, M. 2015. Using mark-recapture distance sampling in aerial surveys of large mammals in south Texas. Thesis Texas A&M University-Kingsville, Kingsville, USA.

Bender, L. C. and M. E. Weisenberger. 2005. Precipitation, density, and population dynamics of desert bighorn sheep on San Andres National Wildlife Refuge, New Mexico. Wildlife Society Bulletin 33:956–964.

Bonier, F. I., T. Moore, P. R. Martin, and R. J. Robertson. 2009. The relationship between fitness and baseline glucocorticoids in a passerine bird. General Comparative Endocrinology 163:208–213

Boonstra, R. 2004. Coping with changing northern environments: the role of the stress axis in birds and mammals. Integrative Comparative Biology 44:95–108.

Boonstra, R. 2013. Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. Functional Ecology 27:11–23.

Breuner, C. W., S. H. Patterson, and T. P. Hahn. 2008. In search of relationships between the acute adrenocortical response and fitness. General and Comparative Endocrinology 157:288–295.

Carr, W. R. 2015. Plants of the South Texas Sand Sheet home. Biosci.utexas.edu. <http://www.bio sci.utexas.edu/prc/digflora/wrc/carr-sandsheet.html>. Accessed 4 Oct 2015.

Cavigelli, S. A. 1999. Behavioral patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. Animal Behaviour 57:935–944.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant., and L. L. Irwin. 2004. Effect of summer-autumn nutrient and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1-61.

Dantzer, B., Q. E. Fletcher, R. Boonstra, and M. J. Sheriff. 2014. Measures of physiological stress: a transparent or opaque window into the status, management and conservation of species. Conservation Physiology 2:1–18.

DeYoung, C. A. 2011. Population dynamics. Pages 147-180 *in* D. G. Hewitt, editor. Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, USA.

East Foundation. 2016. Our land. East Foundation. <http://www.eastfoundation.net/our-land/>. Accessed 4 Oct 2015.

Edmondson, A. J., I. J. Lean, L. D Weaver, T. Farver, and G. Webster. 1989. A body condition scoring chart for Holstein dairy cows. Journal of Dairy Science 72:68–78.

Fulbright, T. E., D. D. Diamond, J. Rappole, and J. Norwine. 1990. The coastal sand plain of Southern Texas. Rangelands 12:337–340.

Gesquirere, L, R., M. Khan, L. Shek, T. L. Wango, E. O. Wango, S. C. Alberts, and J. Altmann. 2008. Coping with a challenging environment: Effects of seasonal variability and reproductive status on glucocorticoid concentrations of female baboons (*Papio cynocephalus*). Hormones and Behavior 54:410–416.

Ginnett, T. F., and E. L. B. Young. 2000. Stochastic recruitment in white-tailed deer along an environmental gradient. Journal of Wildlife Management 64:713–720.

Gwazdauskas. F. C.1985. Effects of climate on reproduction in cattle. Journal of Dairy Science. 68:1568–1578.

Hickling, G., S. M. John and A. R. Moses. 1991. Reproduction and nutrient reserves of bushy-tailed wood rats (*Neotoma cinerea*). Canadian Journal of Zoology 69:3088–3092.

Hines, S. 2016. Deer, cattle, and nilgai interactions. Dissertation, Texas A&M University-Kingsville, Kingsville, USA.

Heddinghaus, T. R. and P. Sabol. 1991. A review of the Palmer Drought Severity Index and where do we go from here? American Meteorological Society 13:242–246.

Huang, J., W. Zhang, J. Zuo, J. Bi, J. Shi, X. Wang, Z. Chang, Z. Huang, S. Yang, B. Zhang, G. Wang, G. Feng, J. Yuan, L. Zhang, H. Zuo, S. Wang, C. Fu, and C. Jifan. 2008. An overview of the semi-arid climate and environment research observatory over the Loess Plateau. Advances in Atmospheric Sciences 25:906–921.

Heffelfinger, J. 2006. Deer of the Southwest. Texas A&M University Press, College Station, USA.

Hewitt, D. G. 2011. Nutrition. Pages 75- 106 *in* D. G. Hewitt, editor. Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, USA.

Huber, S., R. Palme, and W. Arnold. 2003. Effects of season, sex and sample collection on concentrations of fecal cortisol metabolites in red deer (*Cervus elaphus*). General and Comparative Endocrinology 130:48–54.

Jachowski, D. S., B. E. Washburn, and J. J. Millspaugh. 2015. Revisiting the importance of accounting for seasonal and diel rhythms in fecal stress hormone studies. Wildlife Society Bulletin 39:738–75.

Jefferies, B.C. 1961. Body condition scoring and its use in management. Tasmanian Journal of Agriculture 32: 19–21.

Kie, G. K., and M. White. 1985. Population dynamics of white-tailed deer (*Odocoileus virginianus*) on the Welder Wildlife Refuge. Southwestern Naturalist 30:105–118.

Krausman, P. R., J. J. Hervert, and L. L. Ordway. 1985. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71–73.

Kruuk, L.E, T.H. Clutton-Brock, S. D.Albon, J. M. Pemberton, and F. E. Guinness. 1999. Population density affects sex ratio variation in red deer. Nature 399:459–461.

Landys, M. M., M. Ramenofsky, and J. C. Wingfield. 2006. Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. General and Comparative Endocrinology 148:132–149.

Levene, H. 1960. Robust test for equality of variances. Pages 278–292 *in* I. Olkin, editor. Contributions to probability and statistics: Essays in honor of Harold Hotelling. Stanford University Press, Stanford, California, USA.

Lynch, J. W., T. E. Ziegler, and K. B. Strier. 2002. Individual and seasonal variation in fecal testosterone and cortisol levels of wild male tufted capuchin monkeys, *Cebus paella nigritus*. Hormones and Behavior 41:275–287.

Millspaugh, J. J., B. E. Washburn, M. A. Milanick, J. Beringer, L. P. Hansen, and Tamara M. Meyer. 2002. Non-invasive techniques for stress assessment in white-tailed deer. Wildlife Society Bulletin 30:800-907.

Millspaugh, J. J., and B. E. Washburn. 2004. Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation. General and Comparative Endocrinology 138:189-199.

Nakagawa, S. and H. Schielzeth. 2012. A general and simple method for obtaining R2 from generalized linear mixed effects model. Methods in Ecology and Evolution 4:133–142.

National Research Council. 2007. Nutrient requirements of small ruminants: Sheep, goats, cervids, and New World camelids. National Academies Press, Washington, D.C., USA.

Noy-Mier, I. 1973. Desert ecosystems: Environment and producers. Annual Review of Ecology and Systematics 4:25–51.

Ogutu, J. O, and N. Owen-Smith. 2003. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. Ecology Letters 6:412-419.

Owen-Smith, N. 1990. Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. Journal of Animal Ecology. 59:893–913.

Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57–69.

Ragab, R., and C. Prudhomme. 2002. Climate change and water resources management in arid and semi-arid regions: Prospective and challenges for the 21st century. Biosystems Engineering 81:3–34.

Reeder, D. M., and K. M. Kramer. 2005. Stress in free-ranging mammals: Integrating physiology, ecology, and natural history. Journal of Mammalogy 86:225–235.

Romero, L.M., M. Ramenofsky, and J. C. Wingfield. 1997. Season and migration alters the corticosterone response to capture and handling in an Arctic migrant, the white crowned sparrow (*Zonotrichia leucophrys gambelii*). Comparative Biochemistry and Physiology Part C Pharmacology Toxicology Endocrinology 116:171–177.

Sapolsky, R.M. 1986. Endocrine and behavioral correlates of drought in wild olive baboons (*Papio anubis*). American Journal of Primatology 11:217–227.

Sapolsky, R. M., L. M. Romero, and A. U. Munk. 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocrine Reviews 21:55–58.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216.

Shapiro, S. S., and M. B. Wilk. 1965. An analysis of variance test for normality (complete samples). Biometrika 52:591–611.

Sheriff, M. J., C. J. Krebs, and R. Boonstra. 2010. Assessing stress in animal populations: do fecal and plasma glucocorticoids tell the same story? General Comparative Endocrinology 166:614–619.

Sheriff, M. J., B. Dantzer, B. Delehanty, R. Palme, and R. Boonstra. 2011. Measuring stress in wildlife: techniques for quantifying glucocorticoids. Oecologia 166:869–887.

Sheriff, M. J., H. Wheeler, S. A. Donker, C. J. Krebs, R. Palme, D. S. Hik, and R. Boonstra. 2012. Mountain-top and valley-bottom experiences: the stress axis as an integrator of environmental variability in artic ground squirrel populations. Journal of Zoology 287:65–75.

Sivakumar, M. V. K., H. P. Das, and O. Brunini. 2005. Impacts of present and future climate variability and change on agriculture and forestry in the arid and semi-arid tropics. Climatic Change 70:31–72.

Smith, V. D., and L. S. Campbell. 2017. Texas Parks and Wildlife. Exploring Texas Ecoregions. <https://tpwd.texas.gov/publications/pwdpubs/media/pwd_bk_w7000_0030.pdf> Accessed 20 Feb 2017.

Stafford Smith, D. M. 1996. Management of rangelands: paradigms and their limits. Pages 325–357 *in* J. Hodgson and A. Illius, editors. The ecology and management of grazing systems. CABI, Wallingford, United Kingdom.

Texas A&M AgriLife Research and Extension Center. 2015. Annual Report. < http://agrilife.org /lubbock/ files/2016/02/2015-AG-CARES-Report-Website.pdf>. Accessed 12 March 2016.

Texas Parks and Wildlife Department. 2012. Texas Ecoregions. < https://tpwd.texas. gov/education/hunter-education/online-course/wildlife-conservation /texas-ecoregions>. Accessed 12 March 2016.

Texas Water Development Board. 2012. Water for Texas 2012 State Water Plan. < http:// www.twdb.texas.gov/publications/state_water_plan/2012/04.pdf>. Accessed 12 Feb 2018.

Traweek, M., S. Wardroup, J. Williams, and E. L. Young. 1996. The rut in white-tailed deer. <http://tpwd.texas.gov/huntwild/hunt/planning/rut_whitetailed_deer>. Accessed 12 March 2016.

Thornbrugh, C. 2007. Climate, arid and semi-arid regions. Pages 275–276 *in* P. Robbins, editor. Encyclopedia of Environment and Society. SAGE Publications Inc., Thousand Oaks, California, USA.

Tollefson, T. N., L. A. Shipley, W. L. Myers, D. H. Keisler, and N. Dasgupta. 2010. Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. Journal of Wildlife Management 74:974–986.

Verme, L. J., and D. E. Ullrey. 1984. Physiology and nutrition. 91-118 *in* L. K. Halls, editor. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Wasser, S. K., K. E. Hunt, J. L. Brown, K. Cooper, C. M. Crockett, U. Bechert, J. J. Millspaugh, S. Larson, and S. L. Monfort. 2000. A generalized fecal glucorticoid assay for use in a diverse array of nondomestic mammalian and avian species. General Comparative Endocrinology 120:260–275.

Wingfield, J. C., D. L. Maney, C. W. Breuner, J. D. Jacobs, S. Lynn, M. Ramenofsky, and R. D. Richardson. 1998. Ecological bases of hormone behavior interactions: the emergency life-history stage. American Zoology. 3:191–206.

Wingfield, J. C. 1994. Modulation of the adrenocortical response to stress in birds. Pages 121-148 *in* M. D. Stetson, editor. Processing of environmental information in vertebrates. Springer-Verlag, Berlin, Germany.

APPENDIX A

Table A1. Number of lactating and nonlactating female white-tailed deer captured in 4 study sites in 2011 – 2016 in South Texas, USA. Female age class was assigned according to age of last breeding season; yearling (1.5 years old), juvenile (2.5 years old during time of capture) and mature (≥ 3.5 years old during time of capture).

			Lactation status		
Year	Site	Age class	Yes	No	
2011	El Sauz	Yearling	1	16	
		Juvenile	1	4	
		Mature	34	56	
	Santa Rosa	Yearling	0	9	
		Juvenile	0	7	
		Mature	8	35	
	Buena Vista	Yearling	0	5	
		Juvenile	1	6	
		Mature	7	21	
	San Antonio Viejo	Yearling	0	23	
		Juvenile	1	3	
		Mature	22	92	
Total			75	277	352
2012	El Sauz	Yearling	0	12	
		Juvenile	0	13	
		Mature	29	57	
	Santa Rosa	Yearling	0	4	
		Juvenile	1	9	
		Mature	13	45	
	Buena Vista	Yearling	0	4	
		Juvenile	0	26	
		Mature	12	77	
	San Antonio Viejo	Yearling	0	3	
		Juvenile	1	19	
		Mature	20	46	
Total			76	315	391

Table A1. Continued.

			Lactation status		
Year	Site	Age class	Yes	No	
2013	El Sauz	Yearling	0	12	
		Juvenile	2	6	
		Mature	20	64	
	Santa Rosa	Yearling	0	1	
		Juvenile	0	4	
		Mature	8	58	
	Buena Vista	Yearling	0	3	
		Juvenile	0	2	
		Mature	26	44	
	San Antonio Viejo	Yearling	0	9	
		Juvenile	0	10	
		Mature	12	94	
Total			68	307	375
2014	El Sauz	Yearling	0	5	
		Juvenile	1	5	
		Mature	18	46	
	Santa Rosa	Yearling	0	5	
		Juvenile	1	1	
		Mature	20	35	
	Buena Vista	Yearling	0	7	
		Juvenile	0	0	
		Mature	23	31	
	San Antonio Viejo	Yearling	0	2	
		Juvenile	0	5	
		Mature	39	78	
Total			122	220	342
2015	El Sauz	Yearling	0	7	
		Juvenile	3	3	
		Mature	19	18	
	Santa Rosa	Yearling	1	1	
		Juvenile	1	3	
		Mature	8	6	

Table A1. Continued.

			Lactation status		
Year	Site	Age class	Yes	No	
	Buena Vista	Yearling	1	2	
		Juvenile	3	2	
		Mature	8	8	
	San Antonio Viejo	Yearling	0	9	
		Juvenile	3	11	
		Mature	45	40	
Total			92	110	202
2016	El Sauz	Yearling	0	10	
		Juvenile	0	4	
		Mature	5	30	
	Santa Rosa	Yearling	1	4	
		Juvenile	0	1	
		Mature	1	7	
	Buena Vista	Yearling	0	6	
		Juvenile	0	7	
		Mature	2	16	
	San Antonio Viejo	Yearling	0	24	
		Juvenile	2	10	
		Mature	24	74	
Total			35	193	228
					1,594

APPENDIX B.

Table B1. Mean fecal glucocorticoid metabolite concentration (ng/mL) (n) of lactating and nonlactating female white-tailed deer captured on 4 study sites in October and November of 2015 and 2016 in South Texas, USA. Female age class was assigned according to age of last breeding season.

				Lactation status		
Year	Study site	Age class		No	Yes	Mean (ng/mL) (n)
2015	El Sauz	Fawn		96.65 (4)	-	94.95 (4)
		Juvenile		100.94 (2)	158.74 (2)	129.84 (4)
		Mature		133.18 (7)	129.88 (4)	130.16 (11)
			Mean	117.00 (13)	139.50 (6)	122.68 (19)
2015	Santa Rosa	Fawn		155.49 (1)	142.82 (1)	298.30 (2)
		Juvenile		61.38 (2)	-	61.38 (2)
		Mature		133.45 (2)	115.03 (1)	127.31 (3)
			Mean	109.43 (5)	128.93 (2)	115.00 (7)
2015	Buena Vista	Fawn		70.83 (1)	-	70.83 (1)
		Juvenile		72.03 (1)	88.85 (1)	80.44 (2)
		Mature		105.94 (1)	132.59 (3)	121.93 (4)
			Mean	82.93 (3)	121.65 (4)	105.06 (7)
2015	San Antonio Viejo	Fawn		136.24 (1)	-	136.24 (1)
		Juvenile		277.59 (1)	394.617 (1)	336.10(2)
		Mature		147.71 (12)	253.07 (12)	200.39(24)
			Mean	156.17 (14)	263.95 (13)	208.06 (27)
2016	El Sauz	Fawn		88.78 (4)	-	88.78 (4)
		Juvenile		184.02 (1)	-	184.02 (1)
		Mature		161.12 (13)	121.84 (1)	158.31 (14)
			Mean	146.32 (18)	121.84 (1)	145.03 (19)
2016	Santa Rosa	Fawn		-	-	-
		Juvenile		-	-	-
		Mature		-	-	-
			Mean	-	-	-

Table B1. Continued.

Year	Study site	Age class		Lactation status No	Yes	Mean (ng/mL) (n)
2016	Buena Vista	Fawn		141.95 (1)	-	141.95 (1)
		Juvenile		149.69 (2)	-	149.69 (2)
		Mature		118.61 (4)	-	118.61 (4)
			Mean	130.82 (7)	-	130.82 (7)
2016	San Antonio Viejo	Fawn		120.70 (7)	-	120.70 (7)
		Juvenile		167.85 (3)	120.15 (2)	148.77 (5)
		Mature		177.66 (22)	100.27 (8)	157.02 (30)
			Mean	164.28 (32)	104.25 (10)	149.99 (42)

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